



Fisheries and Oceans
Canada

Science

Pêches et Océans
Canada

Sciences

CSAS

Canadian Science Advisory Secretariat

Research Document 2011/095

Maritimes Region

SCCS

Secrétariat canadien de consultation scientifique

Document de recherche 2011/095

Région des Maritimes

Responses of Eelgrass (*Zostera marina* L.) to Stress

Réponses du zostère (*Zostera marina* L.) au stress

Herb Vandermeulen¹, Jolinne Surette², and Marc Skinner³

¹Department of Fisheries and Oceans, Maritimes Region
Bedford Institute of Oceanography
PO Box 1006, Dartmouth, NS B2Y 4A2

²RR#1, Box 3570
Arcadia, NS B0W 1B0

³University of New Brunswick
Department of Biology
Fredericton, NB E3B 5A3

* This series documents the scientific basis for the evaluation of fisheries resources in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

* La présente série documente les bases scientifiques des évaluations des ressources halieutiques du Canada. Elle traite des problèmes courants selon les échéanciers dictés. Les documents qu'elle contient ne doivent pas être considérés comme des énoncés définitifs sur les sujets traités, mais plutôt comme des rapports d'étape sur les études en cours.

Research documents are produced in the official language in which they are provided to the Secretariat.

Les documents de recherche sont publiés dans la langue officielle utilisée dans le manuscrit envoyé au Secrétariat.

This document is available on the Internet at:

Ce document est disponible sur l'Internet à:

<http://www.dfo-mpo.gc.ca/csas/>

ISSN 1499-3848 (Printed / Imprimé)

© Her Majesty the Queen in Right of Canada, 2012
© Sa majesté la Reine, Chef du Canada, 2012

Canada

TABLE OF CONTENTS

Abstract / Résumé	v
Introduction	1
<i>Eelgrass</i>	1
<i>The Model</i>	1
<i>The Stressors</i>	2
Sedimentation	3
Turbidity	6
<i>Direct Effects</i>	6
<i>Indirect Effects</i>	10
Nutrients	10
<i>Direct Effects</i>	11
<i>Indirect Effects</i>	12
Flow Regime	16
Physical Removal	17
Summary	19
<i>Sedimentation</i>	19
<i>Turbidity</i>	20
<i>Nutrients</i>	21
<i>Flow Regime</i>	22
<i>Physical Removal</i>	22
References	22
Tables	34
Figures	42

Correct Citation for this Publication:

Vandermeulen, H., J. Surette, and M. Skinner. 2012. Responses of Eelgrass (*Zostera marina* L.) to Stress. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/095: vi + 43 p.

ABSTRACT

A literature review was performed which included examining approximately 200 publications (most from the primary literature). Those publications fitting our criteria (primarily field studies of adequate duration) were used to describe the responses of eelgrass (*Zostera marina* L.) to stress from five factors. Sedimentation, turbidity, nutrients, water flow regime and physical removal all have the ability to reduce the fish habitat value of eelgrass by increasing meadow patchiness, reducing shoot density or reducing area covered.

The 'HADD' model, used by habitat practitioners applying the Fisheries Act, has terms such as stressor intensity, duration, area scale and frequency - which are difficult to find applied in the scientific literature on eelgrass. As a result, we suggest threshold intensities of the five stressors rather than set absolute values. There is a need to monitor the application of our thresholds and modify them as new data are collated from case studies.

RÉSUMÉ

Une analyse documentaire a été effectuée et consistait à examiner environ 200 publications (dont la plupart étaient issues de publications primaires). Les publications qui satisfaisaient à nos critères (principalement des études sur le terrain d'une durée adéquate) ont été utilisées pour décrire les réponses de la zostère (*Zostera marina* L.) au stress selon cinq facteurs. La sédimentation, la turbidité, les éléments nutritifs, le régime des courants et l'arrachage ont tous la capacité de réduire la valeur de l'habitat du poisson de la zostère en augmentant la microrépartition des herbiers, en réduisant la densité de plants ou la surface couverte.

Le modèle de « DDP* » utilisé par les praticiens de l'habitat qui appliquent la *Loi sur les pêches* utilise des termes tels que l'intensité, la durée, l'ampleur et la fréquence du stressor – dont l'application est difficile à trouver dans les publications scientifiques sur les zostères. Par conséquent, nous proposons de fixer des seuils d'intensité pour les cinq stressors plutôt que d'établir des valeurs absolues. Il faut surveiller l'application de nos seuils et les modifier au fur et à mesure que nous recueillons de nouvelles données issues d'études de cas.

* harmful alteration, disruption or destruction // détérioration, destruction ou perturbation

INTRODUCTION

Eelgrass

Eelgrass (*Zostera marina* L.) is a vascular marine macrophyte found rooted in sandy or muddy substrates. The species occurs on all three Canadian coastlines (den Hartog 1970)¹. The plants can form extensive subtidal, perennial beds (meadows) widely recognized as important nearshore habitat for juvenile (and adult) invertebrates and fish (Short and Wyllie-Echeverria 1996; Chambers et al. 1999). The beds provide cover from predation, reduce local current regimes (allowing for settlement of organisms) and increase secondary productivity by adding to local habitat complexity and surface area (Chambers et al. 1999; Boström et al. 2002; Duarte 2002; Laurel et al. 2003).

The Model

In previous reviews, the lead author explored sensitivity of eelgrass to finfish and shellfish aquaculture (Vandermeulen 2005; Vandermeulen et al. 2006) and discussed eelgrass resilience and persistence (Vandermeulen 2009). In this review, we explored the responses of eelgrass to stress in more detail.

In late 2010, the Regional Science Advisory steering group addressing the issue of "What constitutes a HADD² for eelgrass?" decided upon a framework model. The model provides a way to describe the responses of eelgrass to stress (Fig. 1). As stress increases, a dense continuous bed (or meadow) of eelgrass can respond by becoming patchy, less dense (in terms of shoot / leaf bundle density or leaf count per unit area) or occupy less of the available area. Any combination of these three pathways is possible as stress increases. If stress is unrelenting and intense, the beds can ultimately be destroyed by following these pathways. If stress is reduced, eelgrass beds may fully recover to their pristine state or some point close to it by reversing their position along a path (Fig. 1).

Eelgrass can respond to stress in other ways, such as reduced growth rate of individual leaves or overall photosynthetic rate. However, this review is an attempt to look at habitat scale (meadow or bed scale, tens to hundreds of meters) responses of eelgrass to stressors rather than individual leaf scale responses. Our focus is on patchiness, density and area.

To answer questions pertaining to 'HADD' determinations, the model needs to be applied using Fisheries Act terminology (Fig. 2). In order of increasing severity, the terms are disruption, harmful alteration and destruction. These HADD terms refer to the habitat value of eelgrass meadows for fish and invertebrates, not to the intrinsic 'health' or viability of a population of eelgrass (i.e. a meadow). For the purposes of this paper we have assumed that all eelgrass meadows constitute fish habitat under the Fisheries Act. Therefore, as an eelgrass meadow is increasingly harmed by a stressor its habitat value will move from disruption to harmful alteration to destruction (Fig. 2). The steering group has devised wording to help define what these terms mean for eelgrass under the *Fisheries Act*.

¹ *Ruppia maritima* L. is the other broadly distributed seagrass in Canada (Short et al. 2001). The plants are rather small (usually <20cm) and occur in the upper intertidal or in salt marshes. The west coast also has *Zostera japonica* Ascherson & Graebner (an introduced species), *Phyllospadix scouleri* Hooker and *P. torreyi* S. Watson (Short et al. 2001). *Phyllospadix* is a relatively rare, highly specialized form of seagrass found attached to rocks on wave tossed shores. *Zostera japonica* are small, mainly intertidal plants frequently of annual habit - similar to an intertidal form of *Z. marina* on the east coast, and *Z. noltii* Hornemann in Europe.

² Fisheries Act S35.1 "No person shall carry on any work or undertaking that results in the harmful alteration, disruption or destruction of fish habitat." The acronym HADD comes from the underlined letters.

1. no effect
 - eelgrass bed integrity is not compromised
 - no observable changes in eelgrass structure, within natural variation
2. disruption
 - eelgrass bed can recover its structure and integrity within one year
3. harmful alteration
 - eelgrass can only recover part of its structure and integrity and it will take more than one year to do so
4. destruction
 - eelgrass bed will not survive beyond the season, and will not recover without intervention

Therefore, the fundamental question as it relates to HADD is, 'At what point is the function of eelgrass as fish habitat compromised?', a question we answer here by looking at the response of eelgrass to groups of stressors.

The Stressors

The steering group has decided to focus upon five stress factors (stressors):

1. sedimentation
 - regardless of source
 - eelgrass beds can be damaged by excessive sediment deposition and / or erosion
2. turbidity
 - includes light penetration or water clarity
 - eelgrass is a photosynthetic plant and has a high minimum light requirement for survival
 - the maximum depth of water colonized by eelgrass is determined by the amount of light reaching the bottom
3. nutrients
 - eelgrass is intolerant of anoxic and eutrophic conditions
4. flow regime
 - includes current speed and patterns
 - eelgrass grows best at moderate water currents ($\geq 16 \text{ cm s}^{-1}$) but is unlikely to occur as contiguous beds in conditions of high current
5. physical removal
 - removal of plant blades versus underground rhizomes

Each of these stressors will have an effect upon eelgrass based upon the stressor's intensity, duration, area scale and frequency. Intuitively, Figure 2 addresses the concept of intensity, but the other three terms need a context if we are to proceed. The sedimentation stressor can provide an example. How does an eelgrass bed respond to sedimentation? It depends upon:

- intensity – the rate of sedimentation (e.g. cm per year)
- duration – the amount of time the sediments stay on the eelgrass bed
- area scale – the relative area of the total eelgrass bed covered by the sediment
- frequency – the number of times (per year) that sediments cover the bed

Figure 2 accommodates these four aspects of a particular stressor along the Y-axis, as long as the units of measurement are clear.

In our literature review, we focused on papers that described bed scale responses over ecologically relevant time frames. Field studies with duration of at least three weeks were considered best for extracting HADD threshold values. Large scale laboratory studies (mesocosms) of similar duration were considered acceptable. Short term laboratory studies were used to illustrate general principles rather than to elucidate thresholds.

We used data primarily from studies on eelgrass (*Z. marina*) to generate thresholds. In some instances, data from studies on *Z. noltii* or *Z. capensis* were also used as these temperate seagrasses are relatively similar to some morphs of eelgrass in Canada. Information from tropical seagrasses was used to illustrate general principles, not to develop thresholds.

Sedimentation

If eelgrass is subjected to a rapid sedimentation event, it does not survive resulting burial particularly well. Mills and Fonseca (2003) demonstrated *Z. marina*'s low tolerance to burial. In a field experiment, plants were buried to 0% (0cm), 25% (4cm), 50% (8cm), 75% (12cm) or 100% (16cm) of the average blade height with two different sediment types - sand or silt, to test the intensity (depth of burial) by sediment as a stressor. Their experiment did not test "duration", however, as two different time periods were used in two different experimental designs that measured different end points. Likewise, neither area scale nor frequency were tested.

The only eelgrass response measured by Mills and Fonseca (2003) were leaf metrics. Sheath length³ was not affected, while both leaf length and surface area were reduced by sediment burial.

We used Mills and Fonseca (2003) - see Table 1 - to create our HADD thresholds. Although their experimental results do not allow us to distinguish thresholds for most HADD categories, mortality was observed in a number of treatments and would correspond to "destruction" under the HADD terminology.

At a burial depth as low as 25% of the average above-ground plant height (4cm), Mills and Fonseca (2003) reported that the probability of mortality exceeded 50% in both sediment types. The probability of mortality increased rapidly when burial was 50% of plant height (8cm) - all of the plants in silt sediment were recovered and found to be dead in less than a month. So 50% height can be used as a HADD threshold for destruction via silt burial (Table 1). At 50% burial in sand, some of the plants were found to be alive at the end of the 24 day experiment and complete mortality occurred at 75% sand burial, which can therefore be used as our HADD threshold for destruction via sand burial (Table 1).

Ward et al. (2003) provided time-related information on eelgrass bed destruction related to sediment deposition from a flooding event in the winter of 1992/93 in a river delta. They provide some information on the idea of recovery after burial, as the beds did not recover by the winter of 2000. Apparently, the sediment deposition created mud flats that were too shallow to allow re-colonization of *Z. marina*. Indirectly, Ward et al. (2003) did test for the area scale of the stressor, and they provided an estimate of the area of the eelgrass bed lost. However, they provide insufficient information to derive any HADD thresholds (Table 1).

De Falco et al. (2006) mapped sediment grain size in a bay associated with a port in Italy. They discovered that port dredging activity in the 1970s had caused silt and clay to be deposited in a 5cm thick layer over natural sand sediments in an area just outside of the port entrance. Based

³ Eelgrass leaves occur as bundles bound by a sheath at their common base.

upon field observations, that area should have been covered in seagrass meadows but was now bare. They concluded that the sedimentation event associated with the dredging lead to the absence of the seagrass *Posidonia oceanica* in the area. *P. oceanica* is typically shorter than *Zostera*, so a value of 5cm of burial leading to destruction of the bed is consistent with the values in Table 1.

Cyrus et al. (2008) followed dredger spoil intrusion into an estuary and *Z. capensis* meadow destruction and subsequent regrowth. Fine sediment from a beach based spoil outlet pipe was transported along-shore into the estuary (an unintended destination) where it settled on the leaves of the *Zostera* present, resulting in a major die-back. The sediment washed out of the estuary later, and the *Zostera* beds recovered in less than two years. Only about one centimetre of fine silt was deposited in the estuary by the spoil outlet pipe, and Cyrus et al. (2008) concluded that the death of the *Z. capensis* appeared to be due to light limitation from silt deposition on the leaves rather than burial (Table 1).

Dredging effects on *Zostera marina* were recorded by Sabol et al. (2005). They mapped eelgrass beds with a BioSonics Inc. echo sounder system one year before and then 5 months and 17 months after dredging operations in a small harbour. In the first post-dredging survey, a substantial reduction in coverage occurred in adjoining undredged areas, suggesting possible indirect impacts due to siltation or turbidity from the dredging operations, even though silt curtains had been deployed during dredging. This was followed by a modest recovery between the first and second post-dredging years. However, monitoring of other undredged sites within the region showed natural interannual variations in eelgrass coverage to be almost as large as those occurring at the dredged site.

Erftemeijer and Lewis (2006) reviewed dredging impacts on seagrasses. They divided their analysis of seagrasses into critical thresholds for sedimentation and turbidity – as the two phenomena are often linked as dredging impacts. One of their findings was that *Zostera noltii* appears to be relatively sensitive to sedimentation compared to tropical seagrasses (Table 1). Their turbidity values are reported below.

Everett et al. (1995) tracked sediment movement due to stake based aquaculture of oysters on an eelgrass (*Z. marina*) bed in Oregon, USA. Their main experimental stake plots were created in October 1988 and dismantled in February 1989. The site was monitored from November 1988 through May 1990. Eelgrass cover, shoot density and growth were measured several times over the monitoring period, in both experimental and reference areas. Eelgrass responded negatively rapidly after the establishment of the stake culture, and remained in a depressed state by until at least May 1990 (almost 1.5 y after the stake plot was dismantled). Sediment surface profiles in the stake and reference areas were taken in November 1989. A general deposition of sediment had occurred (approximately 15 cm of sediment deposited in worst area, about 1 to 2m from the center of the stakes). Unfortunately, conclusions regarding sediment deposition alone as the cause of eelgrass loss were not possible in their study. Trampling and entrapment of seaweeds in the area were also listed as contributing factors to eelgrass loss. However, their results were consistent with other work demonstrating sediment deposition in stake style aquaculture (Everett et al. 1995).

In November 1988 Everett et al. (1995) also created some experimental oyster rack culture plots. Eelgrass cover was measured several times during the experiment, in both experimental and reference plots. Eelgrass cover was reduced by rack culture. After nine months into the experiment (July 1989) eelgrass cover was less than 20% under the racks with 100% cover remaining in reference areas. By April 1990 (18 months of rack culture deployment) eelgrass was absent from the experimental rack plots. Sediment surface profiles in the rack and

reference areas were taken in August 1989 (after 9 months of oyster culture). There was a general erosion of sediments around the rack plots (approximately 15cm of sediment was lost in worst area, within about 1m from the center of the experimental racks). Everett et al. (1995) concluded that the loss of eelgrass in the rack area was due to erosion, although shading by the racks may also have been a factor. We analysed their results on sedimentation and erosion effects on eelgrass (Table 1).

Boese and Robbins (2008) examined natural sediment erosion effects on an intertidal eelgrass bed in Oregon. Erosional events were noted by the percentage of shoots with exposed rhizomes in quadrats examined monthly for two years. Winter/spring erosion events were associated with seasonally high river flows and waves. Erosion occurred most intensely at bed margins. Upper mid-intertidal (transition zone) steeper sloped (2.4% slope) shores showed the greatest erosional effects, approaching 50% exposure at some sites. These areas were associated with reduced shoot density and canopy height, plus a higher frequency of flowering (Table 1). Recovery (subsequent reburial of rhizomes by sediment) was not tracked by their study.

Natural sediment erosion on a French beach was tracked by van der Heide et al. (2010). Elongated (parallel to shore) bands of *Zostera noltii* were associated with depressions in a background of sand ripples producing an asymmetric pattern in the depressions where the sea side of the depression was relatively steep sided. In contrast, the coast side more gradually sloped up to normal sediment levels. The *Zostera* occurred on the upward slope of the sea side of the depressions, the newest section of the bed (lower shoot density) being on the sea side edge, while the older portions of the bed (higher shoot density) were found at the deepest portion of the depression towards the coast side. The maximum depth of these depressions was 6.5 cm, similar to mean *Z. noltii* rooting depth, suggesting that shoots were being eroded in these depressions – this was confirmed by the presence of a higher proportion of uprooted shoots at this point (Table 1). An average net seaward migration of approximately 17 cm per year was recorded for the seagrass bands. The *Zostera* itself appeared to be forming these depressions, as removing the plants allowed the depressions to disappear within two tidal cycles. Adding artificial seagrass blades to the sand caused depressions to form (van der Heide et al. 2010).

Long term sedimentation rates are commonly determined by examining sediment cores collected at field sites. Microfossils and isotopes in the sediments can be used to age the sediment layers and reconstruct past biotic assemblages in the area. Cooper and Brush (1993) used these methods in Chesapeake Bay. In a similar study, Cooper et al. (2004) examined two estuaries in North Carolina. Both papers contain similar results, pre-industrial sedimentation rates in these estuaries were around 0.1 cm per year, corresponding to a diatom community indicative of healthy submerged aquatic vegetation (like eelgrass). With intensification of land use (starting as early as the late 1700s for Chesapeake Bay), sedimentation rates increased and the diatom community changed to one indicating a lack of submerged aquatic vegetation, corresponding with known losses of eelgrass through time. A sedimentation rate of approximately >0.5 cm per year corresponded with the loss of submerged aquatic vegetation (Table 1). Note that this observation is a correlation, and the sedimentation rate could be a proxy for anthropogenic impacts in general.

Sediment dumping (e.g. as a result of dredging operations) causes elevated suspended solids levels in the water column. Burial harms eelgrass, but so too can the presence of suspended solids without immediate burial. Lee (1997) experimentally manipulated suspended solids levels in *Z. japonica* clumps by adding approximately 2.29 mg of dry silt per square centimetre of clump area per day for three months. The clumps / patches were part of a large intertidal bed,

so the silt addition was in addition to background silt deposition. Although both percent cover and dry weight of the *Z. japonica* decreased, the results were not significantly different from controls (Table 1).

Turbidity

van der Heide et al. (2009) examined data from 79 western European sites and determined that the presence or absence of *Zostera marina* can be predicted quite confidently by light attenuation and sediment redox. Turbid waters are one of the main factors causing the loss of eelgrass. In their review of the effects of reduced light on seagrasses, Leoni et al. (2008) provide a model diagram indicating the most common responses of seagrasses to light (turbidity) stress. In this model, as the duration and intensity of light deprivation increases seagrasses will express a number of physiological and morphological responses. As the turbidity stress increases the plants will reduce their carbon reserves and start to lose biomass, growth, shoot density and area coverage – death is the ultimate endpoint.

Daniell et al. (2008) surveyed sand bank movement in the shallow waters of Torres Strait in north Australia. Seagrass communities (primarily *Cymodocea* and *Halophilla*) were known to disappear in this area periodically and burial by sand bank movement was considered a possible mechanism for the die backs. Using detailed repeat multibeam sonar surveys, they discovered that no consistent current driven direct burial pattern was to blame over the scale of the survey area. The authors concluded that high levels of water column turbidity at the end of the monsoon season (unrelated to local current activity) was a more likely mechanism for sporadic Torres Strait seagrass dieback.

There are a wide variety of factors that can cause water column turbidity, which reduce light levels at depths where seagrasses would otherwise normally grow:

- Suspended solids absorb and reflect available light;
- Point and non-point sources of turbidity and coloured chemicals can be found both nearshore and offshore (there are natural and anthropogenic sources);
- Detrimental shading of eelgrass by light attenuation in the water column due to "brown tide" (e.g. *Aureococcus anophagefferens*, blooms of which do not appear to be related to eutrophication; Bricelj and Lonsdale (1997);
- Rivers dark with naturally occurring dissolved humic acid and other suspended organic compounds and detritus can discharge into estuaries;
- Dredging and shoreline construction can create plumes of turbid water;
- The 'footprint' of support structures for marine activity (docks, wharves, floats, vessels, etc.) includes local shading of the bottom. This effect is not trivial if the support structure is large and the underlying water depth is shallow.

Direct Effects

Even if eelgrass is not buried by sedimentation, excessive amounts of particulate material settling on leaves can lead to plant mortality. The mechanism for damage appears to be reduced photosynthesis due to shading of leaves by the deposition of particulate material (Tamaki et al. 2002). The stressor in this instance is turbidity (loss of light).

The transplantation experiment of Tamaki et al. (2002) lasted from December 1997 through August 1998. During this time period, transplants in a reference area (their station #1) maintained a 100% survival rate while transplants at Station #3 had approximately 20% survival by the end of the experiment and transplants at Station #4 suffered complete mortality within

two months of the start of the experiment and did not recover. Station #1 was in the center of an eelgrass meadow, Station #3 at the edge, and Station #4 just outside. Both suspended solids in the water column and deposition of material on the eelgrass leaves increased moving from stations 1 through 4. Due to this material, photosynthetic photon flux density (PPFD) was reduced to 84% (of that available without this deposition) at Station #1 and to only 36% at Station #4. The low PPFD at Station #4 was linked to the decimation of the transplants at that site. An analysis of the data in Tamaki et al. (2002) is provided in Table 2.

Chronic high spring season turbidity was cited as the primary factor preventing the re-establishment of healthy eelgrass beds in a portion of Chesapeake Bay associated with the York River (Moore et al. 1996). They performed transplants in the fall of 1984, 1985 and 1986 to sites which had eelgrass in 1970 (i.e. lower turbidity levels at that time) but now had few or no plants, plus reference sites. There was a steady decline in survival at non-reference sites and it took approximately half a year for the transplants to die at the worst sites. Spring total suspended solids in the water column were often well over 20 mg l^{-1} at the worst upstream site. This led to light attenuation coefficients of over $2 K_d \text{ m}^{-1}$, almost double that found in the more pristine reference sites. At that light attenuation level the photosynthetically available radiation (PAR) at transplant depth at the worst site was only 12% of sub-surface irradiance. The import of these observations is summarized in Table 2.

Both light and current effects on *Zostera noltii* were examined in a 46 day mesocosm study by de los Santos et al. (2010). Their 'limiting light' level was $2.5 \text{ mol photons m}^{-2} \text{ d}^{-1}$, and 'saturating light' was set to $15.6 \text{ mol photons m}^{-2} \text{ d}^{-1}$. Survival, biomass and root metrics all decreased significantly under limiting light conditions (Table 2).

Ochieng et al. (2010) used an 81 day mesocosm study on *Z. marina* with four light treatments (100, 58, 34 and 11% of surface irradiance - SI). The 11% of SI treatment resulted in 81% mortality. The plants persisted at 58% SI and above, and were light limited at 34% SI and below (Table 2).

Short et al. (1995) used mesocosms to observe the effects of reduced light intensity (shading) over four months on the shoot density, leaves per shoot, and leaf length and width of *Zostera marina*. Interestingly, leaf length increased at low light while shoot density decreased⁴. There was an overall reduction in biomass at lower light levels. Short et al. (1995) consider 10 to 20% of surface light as the minimum light limit for eelgrass survival (Table 2).

In another shading experiment, Lee (1997) used two different densities of black plastic mesh to shade small patches of a *Zostera japonica* bed for three months. The two shades reduced average irradiance by 55-65%. The shaded plots had reduced percentage cover and dry weight biomass of seagrass compared to reference sites, but the differences were not significant (Table 2).

Mesh screening was also used in situ by Philippart (1995) over one growing season (May through October 1989). She found that if intertidal *Z. noltii* is shaded to 15% of ambient light levels, leaf loss rate increases dramatically and the leaf net growth rate becomes negative. Thirty percent shading still allowed for some growth (Philippart 1995). Although Philippart's experiment did not include the 'recovery' factor as the reduced light regimes were held constant for the duration of the experiment, there is a possibility to use her results to estimate the HADD term 'disruption'. At a shading level of 30% of ambient, the seagrass plants were not destroyed, but they were negatively impacted (Table 2).

⁴ Newell and Koch (2004) provide evidence that shoot density will increase in *Ruppia* beds if water column turbidity is reduced.

Carroll et al. (2008) combined field observations with an in situ shading experiment on *Z. marina*. They observed a productivity reduction of approximately 50% for plants in meadows occurring in waters with extinction coefficients of 1.5 to >2.5 versus meadows in waters with lower K_d values (<1.5). In their 35 day long shading experiment, plots with Vexar™ mesh (40% reduction in ambient light) also had significantly reduced production over controls, as well as a significantly reduced number of leaves per shoot and leaf area (Table 2)⁵.

Holmer and Laursen (2002) used two week long laboratory shading experiments to record reduced shoot density and leaves per shoot in spring collected eelgrass plants exposed to 20 – 25 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ light levels. Plants collected in the fall were less sensitive to these reduced light levels. They found that shaded eelgrass growing in low-organic sediments appeared to be incapable of assisting in the reoxidation of sulphides, leading to anoxic and sulphide laden pore water conditions which may further reduce growth and survival. The results of Holmer and Laursen (2002) are consistent with other authors, but their experiment was very short term and we could not use their results in Table 2.

Peralta et al. (2003) ran a two month long laboratory shading experiment on *Zostera marina*. They used 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ as 'saturating' light levels and 55 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ as 'subsaturating' in their experiment. Plants under subsaturating light accumulated lower biomass than those grown at saturating level irrespective of sediment enrichment conditions. The plants under subsaturating light also lost more leaves. The subsaturating light level had a negative effect over the two month period, but did not destroy the plants. Their two-month time frame was sufficiently long to conclude that the subsaturating light level could be used as a 'disruption' or even 'harmful alteration' value in our HADD model (Table 2).

Brun et al. (2008) performed a 21 day laboratory experiment with *Zostera noltii* which manipulated light and nutrients. They set 'saturating light' at 220 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and 'limiting light' at 25 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. At the end of the experiment net production was negative for the plants grown under 'limiting light', irrespective of nutrient conditions. Sucrose levels in above ground and below ground tissues were significantly lower under the limiting light conditions compared to saturating light. In this instance, the limiting light regime was definitely harmful to the plants (Table 2)⁶.

Biber et al. (2009) ran a seven week laboratory experiment on light deprivation and recovery for *Zostera marina*. The treatments were light control, dark control, three days of dark followed by nine days of light (3D:9L) and repeated, 3D:3L, 9D:9L and 9D:3L. On light days, the diel light cycle was 14L:10D with light exposure during light periods set at 75 to 100 $\mu\text{E m}^{-2} \text{s}^{-1}$ (i.e. same $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), 20-25°C – that cycle and light intensity would allow for normal growth of *Z. marina*. In terms of mortality, all treatments had approximately the same death rates (approximately 10% or so) except that death of plants was observed in darker controls - 9D:3L (about 50% mortality) and total darkness (100% mortality). *Zostera* seedlings were more sensitive to lack of light compared to mature plants. Shoot density was reduced or variable under the different treatments for mature plants. Seedlings were more impacted, especially losing shoots under the 9D treatments. Seedlings and mature plants lost shoots under the dark control treatment. Leaves per shoot, biomass and leaf length followed similar patterns. Overall, the 3D:9L pattern was quite similar to the light control results, but the 9D:9L and 9D:3L results

⁵ Collier et al. (2009) ran in situ shading experiments in a *Posidonia sinuosa* meadow. At shading levels below minimum light requirements, complete shoot loss could take up to two years. They estimate that recovery after shading would take 3.5 to 5 years.

⁶ In a very similar experiment, Olivé et al. (2009) manipulated the effects of light and sediment organic matter on *Zostera noltii*. The effects of sediment organic matter overwhelmed the results (see 'Nutrient' section below).

suggest a downward decline towards the dark control (i.e. death). *Zostera* (especially seedlings) does not recover well after nine days of darkness (Table 2).

Storm induced water column turbidity reduced light levels to near zero for more than three weeks over a coastal eelgrass bed in a study in Baja California, where light attenuation coefficient values reached $2 K_d \text{ m}^{-1}$ (Table 2) and the plants died after sugar and starch content in the leaves decreased by ~85% (Cabello-Pasini et al. 2002).

In a related study, Cabello-Pasini et al. (2003) examined the effect of irradiance in three other lagoons in the Baja area. They measured shoot density, biomass, leaf metrics and photosynthesis of *Z. marina*. The beds appeared to be light limited for 15% of the year (during winter) in one of the lagoons, which had approximately half the irradiance of the two other sites. The 'low light' lagoon had high turbidity due to fine silt resuspended by wind events, and winter sediment loads from river flow. Light attenuation coefficients in the two lagoons were consistently below $0.5 K_d \text{ m}^{-1}$ year round, while the 'low light' lagoon had most values over $1 K_d \text{ m}^{-1}$ and some over 1.5 or $2 K_d \text{ m}^{-1}$.

Table 2 summarizes these results. In their study, the low light lagoon had high, but quite variable, biomass of eelgrass during the summer months, but dropped off quite rapidly during the winter. As in Short et al. (1995), a low light regime seems to cause an increase in leaf length, suggesting that plants are compensating for low light levels by elongating their leaves towards the surface of the water column (Cabello-Pasini et al. 2003). Since the eelgrass beds in the low light lagoon were seasonally depressed and then recovered based upon light levels, the 'duration' aspect of the turbidity stressor was tested and it is possible to deduce a 'disruption' threshold (Table 2).

In their review of impacts of dredging on seagrasses, Erftemeijer and Lewis (2006) determined that *Z. marina* requires quite high light levels to survive (Table 2). Moreover, *Zostera* species (*Z. capricorni* & *Z. noltii*) do not tolerate low light levels for long compared to other seagrass species. The plants may only survive for a month or less at minimum required light requirement levels⁷.

Laboratory experiments on the photosynthetic physiology of seagrasses provide some empirical evidence supporting the results observed during the studies mentioned above. In a study calculating standard photosynthesis versus irradiance curves (P-I curves) for eelgrass, Marsh et al. (1986) found that the photosynthetic compensation point (oxygen production = oxygen consumption) occurred at about $3 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ at 10°C and about $17 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ at 20°C . Saturating light levels were at 36 and $78 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, respectively. These values fall within the same range and end points as those we show in Table 2.

Thom and Southard (2008) measured photosynthetic rates of *Z. marina* at a variety of locations and depths in Washington and Oregon estuaries. They suggest a compensation point irradiance of approximately $50 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ and provide estimates of integrated daily average light requirements for long term survival (Table 2).

The estimated daily compensation point of young *Z. marina* was calculated as 5.7% of sea surface light by Abe et al. (2003). This value is somewhat low compared to those listed in Table 2, but the time frame of their laboratory test was short and the compensation point was model based. Using similar methods Abe et al. (2010) determined that *Z. japonica* has slightly

⁷ van der Heide et al. (2010) describe a dynamic beach where water column turbidity was too high to allow *Zostera noltii* growth during submersion. The plants appeared to survive by photosynthesizing during low tide. The optimal position of the seagrass on the shore was driven by light limitation and desiccation gradients with depth.

higher light requirements than *Z. marina*. They surmised that this difference explains why *Z. japonica* occurs in shallower habitats than *Z. marina*.

Boese et al. (2005) performed outdoor measurements of photosynthesis on *Z. marina* blades which are consistent with the findings of Abe et al. (2010). They record a saturating irradiance of approximately $65 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ for perennial plants and $171 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ for annual plants higher up in the intertidal.

In their review of irradiance requirements for *Z. marina* growth, Boese et al. (2005) reported a wide range of values needed to saturate photosynthesis, 7 to $385 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ from literature sources. Lee et al. (2007) reviewed minimum light requirements for eelgrass and also found a wide range of values, from 11 to ~30% of surface irradiance. Lee et al. (2007) stated that this variability was likely attributed to photo-acclimation to local light regimes. These reviews suggest the need for site-specific estimates of eelgrass photosynthetic performance prior to making a determination of HADD status on the basis of water column light levels alone.

Indirect Effects

The water column itself does not have to be 'dark' to shade marine macrophytes. Eelgrass and seaweeds can become indirectly shaded at their surfaces by epiphytes growing on them. Hauxwell et al. (2001) report that approximately 2 mg cm^{-2} of epiphytic material on *Z. marina* leaves can reduce leaf surface light levels by 31% and about 8 mg cm^{-2} of epiphytic material reduced surface light by 63%.

Drake et al. (2003) found that epiphytes were absorbing about 40% of the light available at photosynthetically active wavelengths to the eelgrass leaves at an epiphyte biomass of approximately $110 \mu\text{g C cm}^{-2}$. These levels could reduce photosynthetic rates of eelgrass leaves by 49%.

Therefore, additional shading effect of epiphyte load should be considered when calculating HADD effects on eelgrass meadows due to reduced light⁸. Kemp et al. (2004) have developed a model to accommodate both water column light attenuation and epiphyte based light attenuation for calculating maximal depth limits for seagrasses (primarily eelgrass and *Ruppia*).

Nutrients

Eutrophication has been defined by Nixon (1995) as an increase in the rate of supply of organic matter to an ecosystem and the resulting increase in nutrients. In contrast with anthropogenic increases to nutrients in freshwater environments, marine eutrophication is a relatively new anthropogenic phenomenon, but one which has been growing over time (Nixon 1995). Short and Wyllie-Echeverria (1996) concluded that anthropogenic nutrient inputs to coastal areas is the primary cause of the present world-wide decline in seagrasses. The decline will likely accelerate in the future (Duarte 2002) if current inputs continue. Deeper eelgrass beds appear to respond to the negative effects of eutrophication more predictably than shallow beds (Frederiksen et al. 2004).

Lotze et al. (2003) surveyed a number of eelgrass beds along the southern shore of the Northumberland Strait (New Brunswick). They determined that bays with nutrient loading (including those from aquaculture sources) coincided with negative impacts on eelgrass beds.

⁸ Epiphytes are also considered in the discussion of nutrients, below.

We describe the responses of eelgrass to eutrophication below. As a starting point, Lee et al. (2004) argued that area normalized leaf mass ($\text{mg dry weight cm}^{-2}$) may be the best index of *Zostera marina* response to estuarine eutrophication. They found that this index was superior to more classically used morphometrics – e.g. number of leaves per shoot, blade width and leaf length.

Interestingly, the $\delta^{15}\text{N}$ tissue residues in *Z. capricorni* reflected the source of nitrogen loading in Moreton Bay, Australia (Udy and Dennison 1997). It was possible to discriminate between prawn-farm aquaculture and sewage effluent nitrogen sources from the stable isotope tissue residues in the plants.

Direct Effects

Elevated nutrient concentrations can have *direct* physiological effects on marine plants (e.g. elevated tissue residue concentrations, growth and development of reproductive tissues). Eelgrass is very effective in removing nitrogen from sediment and the water column for growth (Pedersen and Borum 1992). *Zostera* growth can be reduced by naturally occurring nutrient limitation (Boström et al. 2004; Carroll et al. 2008).

Burkholder et al. (1992) used an outdoor mesocosm system to determine that eelgrass may be affected by direct toxicity at even 'low' nitrate loading rates of $3.5 \mu\text{M NO}_3^- \text{-N day}^{-1}$. The nitrate appeared to damage the plants' meristems and led to leaf loss. Unfortunately, their experimental design did not control for important factors such as the growth of herbivores and algae in the mesocosms (Table 3). Water column nitrate toxicity was also reported by Touchette et al. (2003). Their mesocosm experiments did control for benthic algal growth, but not epiphytes.

Burkholder et al. (1994) conclude from outdoor mesocosm experiments (not controlled for algal growth) that elevated nitrate levels in nearshore waters due to eutrophication (c.a. 5 to $10 \mu\text{M NO}_3^- \text{-N day}^{-1}$) will have a direct adverse effect on *Zostera marina* (Table 3).

Peralta et al. (2003) used indoor mesocosms over two months and found that high porewater nitrate concentrations (20 mM) inhibited *Z. marina* growth (Table 3). This corroborates the findings of Burkholder et al. (1992) and Touchette et al. (2003) on water column based nitrate toxicity.

Williams and Ruckelshaus (1993) found a positive relationship between *Zostera marina* shoot growth rates and pore water ammonium concentration. The half saturation constant was $96 \mu\text{mol L}^{-1}$, and no inhibitory effects were seen even at pore water ammonium concentrations $\sim 2000 \mu\text{mol L}^{-1}$. However, Kaldy et al. (2004), report that high sediment ammonium concentrations can be toxic to some vascular marine macrophytes.

Direct ammonium toxicity to *Zostera noltii* was noted by Brun et al. (2008). This affect was lessened greatly if the plants were nutritionally replete with phosphorus prior to ammonium exposure⁹. Cabaço et al. (2008) record direct ammonium toxicity for *Zostera noltii* in the field due to urban wastewater discharge (Table 3).

⁹ van der Heide et al. (2008) tested ammonium toxicity in the lab and discovered that the effect could also be reduced greatly if high densities of *Z. marina* shoots were employed in the experiment. The toxic effect appeared to be buffered by joint ammonium uptake at high shoot density.

Indirect Effects

The *indirect* effects of elevated nutrient concentrations in a water column (i.e. eutrophication) include elevated turbidity due to stimulation of phytoplankton growth, increased algal epiphyte load, alterations in geochemistry, shifts in macrophyte species composition and low oxygen levels:

i) Elevated Turbidity due to Stimulation of Phytoplankton Growth

The eutrophication of coastal waters can lead to the stimulation of phytoplankton growth and a subsequent increase in water column turbidity. The turbidity effect¹⁰ of eutrophication can result in reduced water column light levels which negatively impact eelgrass and macrophyte growth (Pedersen 1995; Kemp et al. 2004).

ii) Increased Algal Epiphyte Load

Under normal conditions, grazers remove epiphytic algae from seagrass leaves and improve growing conditions for the seagrass (Hily et al. 2004). However, under eutrophic conditions, epiphytes and macroalgae can seasonally outgrow grazing rate by herbivores (Burkholder et al. 1992), or selective grazing can allow certain epiphyte species to bloom (Duffy and Harvilicz 2001). The presence of excessive epiphyte growth can be detrimental to *Zostera*. For example, Williams and Ruckelshaus (1993) report that increasing epiphyte load from 50 to approximately 200 mg per eelgrass shoot reduced shoot growth rates from approximately 1 cm shoot⁻¹d⁻¹ to 0.2 cm shoot⁻¹d⁻¹.

The inhibitory effect of epiphytes comes in the form of shading (Burkholder et al. 1992; Short et al. 1995; Hauxwell et al. 2001; Brush and Nixon 2002; Kemp et al. 2004), interference with nutrient uptake (Hauxwell et al. 2001), and interference with carbon uptake (Sand-Jensen 1977).

iii) Alterations in Geochemistry

As noted above, eelgrass rhizomes are effective in removing nutrients from sediment. If *Zostera* dies back in an area due to eutrophication of the water column, sediment nutrient concentrations are likely to increase as an indirect response to plant loss.

Eutrophication from sources as varied as fish farms and sewage treatment plants can cause elevated carbon content in sediment, lowered oxygen concentrations, elevated hydrogen sulphide concentrations, negative redox potential, mobilization of metals and nutrients, etc. (Rozan et al. 2002). These nutrient driven changes may result in negative effects for rooted marine plants like seagrass (e.g. Cancemi et al. 2003; Apostolaki et al. 2009). Olivé et al. (2009) demonstrated that alterations in sediment geochemistry may affect *Z. noltii* more profoundly than alterations in light regime.

Eelgrass can reduce daytime hydrogen sulphide concentrations in sediment pore water (Hebert and Morse 2003)¹¹. *Zostera* can also buffer broader aspects of sediment geochemistry in the face of moderate eutrophication. However, the capacity of plants to process nutrients and buffer some eutrophic conditions can be exceeded and become detrimental to the plants themselves (de Wit et al. 2001; Holmer et al. 2009b).

¹⁰ For a broader discussion of turbidity as a stressor see detailed section above

¹¹ Similar reductions are observed in other seagrass species as well (Holmer et al. 2009c).

Eelgrass rhizomes are protected from damage by hydrogen sulphide in sediment pore water via a supply of oxygen from the leaves to the rhizomes along hollow channels called lacunae. At water column oxygen levels of below 20% saturation, the lacunal system is incapable of providing sufficient oxygen for sulphide re-oxidation, and the hydrogen sulphide concentration in the rhizomes can rise rapidly and may become toxic (Pedersen et al. 2004).

Terrados et al. (1999) experimentally altered sediment geochemistry in situ with the addition of sucrose (i.e. spiking the sediment with a carbon load, emulating eutrophication). After three months, the subsequent increase in pore water sulphide levels (over 70 μM H_2S) and reduction in sediment redox potential caused reduced leaf growth in *Z. marina*, shoot density was unaffected. The length of their experiment allowed us to estimate the 'disruption' threshold for hydrogen sulphide (Table 3).

Goodman et al. (1995) demonstrated that elevated sediment sulphide and reduced light availability due to eutrophication had an additive inhibitory influence on *Z. marina* in a 21 day mesocosm experiment. A combination of high sediment sulphide concentration (800 – 1000 μM) and low light (15% of solar irradiance) reduced photosynthetic rates to about one tenth that observed under high light (50% of solar irradiance) and low sulphide (below 400 μM) conditions. Elevated sediment sulphide had the potential to reduce photosynthetic rates at any light level (Table 3).

Under degraded conditions associated with excess nutrient loading, eelgrass may be replaced by algal mats or canopies (Hauxwell et al. 2001). Sfriso and Marcomini (1999) found that the sediment nutrient (nitrogen and phosphorus) recycling capability of *Ulva* algal mats was at least an order of magnitude lower than the capacity of *Zostera* dominated areas.

Iv) Shifts in Macrophyte Species Composition

Shifts in species composition can occur along eutrophication gradients. As nutrient loading increases, slow growing seagrasses and macroalgae are replaced by fast growing algae, with phytoplankton dominating at the highest loading rates (Duarte 1995).

In flow-through mesocosm experiments, Karez et al. (2004) demonstrated that enrichment from 1 to 32 μM dissolved inorganic nitrogen (with 0.06 to 2.0 μM dissolved inorganic phosphorus) selectively influenced the growth of foliose algae. Corticated filamentous algae tended to decline and foliose algae became more predominant as nutrient levels increased. This effect was partially mediated by an increase in herbivore numbers at the higher nutrient treatments, preventing ephemeral algae from developing high biomass at high nutrient levels. *Ulva* (a foliose alga) dominated at the higher nutrient level treatments. Nitrate-based eutrophication may especially favour the overgrowth of green algae (*Ulva* or *Enteromorpha*) over eelgrass (Harlin and Thorne-Miller 1981).

Patricio et al. (2004) described seagrass distribution exposed to an eutrophication gradient in the Mondego estuary in Portugal. The non-eutrophic portion of the gradient had *Zostera noltii* meadows, *Z. noltii* was absent in the intermediate eutrophic section; periodic abundance of macroalgae and *Enteromorpha* blooms occurred regularly in the highly eutrophic section.

In 1998, hydrodynamic alterations in Mondego estuary resulted in a 40-50% reduction of dissolved inorganic nitrogen in the water column (primarily a reduction in ammonium). Lillebø et al. (2005) monitored both the collapse of the *Z. noltii* beds from 1993 to 1997, and their subsequent resurgence from 1999 through 2003. More recently, Cardoso et al. (2010)

summarized the effects of the nutrient management efforts in Mondego estuary¹². They confirm that the reduction in nitrogen loading was associated with reduced green algal blooms and a resurgence of the area covered by the *Zostera noltii* meadows (Table 3).

Laboratory-based mesocosm experiments by Martínez-Lüscher and Holmer (2010) demonstrated the impacts of the red seaweed *Gracilaria* on *Z. marina*. They overlaid eelgrass shoots with 'low' (loose mat 8cm thick, 2.2 kg wet wt m⁻²) or 'high' (dense mat 10cm thick, 4.0 kg wet wt m⁻²) loads of *Gracilaria* at various temperatures. Sulphide in porewater increased with the high *Gracilaria* load at most temperatures. Eelgrass survival rates showed a decreasing trend with algal biomass, especially at higher temperatures (26 and 30 °C). Survival was reduced to 21% in the high *Gracilaria* load treatments at 26 °C. Such temperatures are common during the summer months (when algal biomass is high) in Atlantic Canadian estuaries (Table 3).

Cummins et al. (2004) used a field cage plot experiment in Australia to demonstrate that typical *Enteromorpha* bloom biomass (c.a. 4.5 kg wet wt m⁻²) led to >50% reductions in seagrass (*Halophila ovalis*, *Z. capricorni*, *Ruppia megacarpa*) biomass after three months in a meadow affected by such a bloom¹³. The reduction in seagrass biomass in their study was quite severe and could be considered a 'harmful alteration'; although recovery was not tested (Table 3).

Deegan et al. (2002) reported that as nitrogen load increased in a series of estuarine ponds (16 to 1679 kg N y⁻¹), macroalgal biomass increased and eelgrass shoot density and biomass decreased, leading to declines in fish and decapod abundance and biomass as well as declines in fish species diversity. Moreover, $\delta^{15}\text{N}$ values indicated that fish were not linked to a food web based on macroalgae, and grew faster and had greater survivorship in eelgrass compared to macroalgal habitats. Over time, eelgrass meadows produce more plant biomass than macroalgal areas driven by eutrophication (Dolbeth et al. 2003).

Deegan et al. (2002) demonstrated through field manipulations that a macroalgal cover of approximately 100 g dry wt m⁻² over an eelgrass bed could prevent the bed from growing (increasing shoot density)¹⁴. Since this effect was seen over a one year period with no recovery from the eelgrass bed, it could be considered a 'harmful alteration' (Table 3).

In their study area in the Seto Inland Sea (Japan), Sugimoto et al. (2007) used field observations at transplant and seeded plots plus outdoor mesocosms to document the harmful effects of *Ulva* accumulation on *Z. marina*. *Ulva* can cover the bottom in 20-30 cm thick mats at their site. No eelgrass seedlings were found at their seeded field site when *Ulva* canopy height was greater than 20 cm; even 10 cm of *Ulva* canopy had quite strong inhibitory effects on seed germination¹⁵. Mesocosms with 13 cm *Ulva* canopy showed little difference from controls in terms of eelgrass survival, while seedling growth was strongly inhibited. Mesocosms with 25 cm *Ulva* canopy showed 100% eelgrass mortality in 38 days (Table 3).

Holmer and Nielsen (2007) used laboratory based mesocosm experiments to demonstrate harm to *Zostera marina* shoots from 5 and 10 cm thick filamentous algal mats (*Ceramium* spp.). The mats created anoxic conditions in the underlying sediments and increased sulphide levels. After three weeks, the eelgrass shoot growth rates were reduced and plants showed signs of

¹² Similar results are presented by Leston et al. (2008).

¹³ In a more tropical situation, Houk and Camacho (2010) make the link between coastal eutrophication and subsequent increases in seaweed canopy with concomitant seagrass (*Halodule*) decline.

¹⁴ Boese and Robbins (2008) record *Ulva* dry weights of 300 to 700g dry wt m⁻² corresponding to seasonal reductions in eelgrass shoot density, but causality was not proven.

¹⁵ Although smothering by algal mats may be the main inhibitory effect, Valdemarsen et al. (2010) found that at least 40% of eelgrass seedling mortality at their study site could be accounted for by drifting macroalgae (mainly *Fucus*) scouring the bottom, inhibiting eelgrass growth and survival.

degradation, even with only 5 cm of algal cover (Table 3). Tissue measurements indicated sulphide invasion into the roots, leading to the reduced growth.

Short and Burdick (1996) recorded a steady decline in *Zostera marina* in Waquoit Bay, Massachusetts over a five year period. The decline was related to housing development and subsequent increases in nitrogen loading in groundwater. The resulting eutrophication stimulated algae (epiphytes, macrophytic algae, and phytoplankton) which shaded the eelgrass, leading to these declines.

Hauxwell et al. (2001) compared two estuaries in Waquoit Bay, one with a loading of $5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and the other with $30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. At the higher loading rate, a macroalgal canopy grew along the bottom which interfered with eelgrass growth. Using in situ manipulations (May through September 1998), they identified a 9 – 12cm critical macroalgal canopy height at which eelgrass declines (Table 3). Most of this effect was due to light limitation of eelgrass by macroalgal canopy shading, but unfavourable biogeochemical conditions were also generated¹⁶. Hauxwell et al. (2001) also present data from three estuaries which demonstrate that *Z. marina* will not be present when nitrogen loading rates per hectare of estuarine area are $300 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ or higher.

In general, nutrient loading rates of approximately $\leq 10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ appear to have no major effect on eelgrass beds in Waquoit Bay estuaries, about $30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ will lead to substantial eelgrass loss (80 to 96% of bed area) and $\geq 60 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ will cause total disappearance (Short and Burdick 1996; van Katwijk et al. 1999; Hauxwell et al. 2003; Hauxwell et al. 2006). See Table 3 for a summary¹⁷.

The negative effects of the macroalgal canopy under nutrient loading are the primary mediator for eelgrass decline in these estuaries (Hauxwell et al. 2006). Fox et al. (2008) revisited the Waquoit Bay dataset and confirmed that eelgrass was absent for the six years of the study in water bodies with loadings of 601 and 403 $\text{kg N ha}^{-1} \text{ yr}^{-1}$ and present for the six years in a local water body with a loading rate of $12 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Table 3).

Vaudrey et al. (2010) document the decimation of an eelgrass bed in a small cove in Long Island Sound subject to long term municipal wastewater discharge. *Ulva* dominated the flora of the cove at loading rates of approximately $185 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. The removal of the wastewater outfall resulted in a reduction of total N input to approximately $90 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, with a subsequent long term and pronounced decline in *Ulva* biomass, leading to a substantive recovery of the eelgrass bed (Table 3).

Latimer and Rego (2010) analysed data from 62 estuaries in New England and concluded that at a loading rate of $\leq 50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, eelgrass extent is variable and is likely controlled by other ecosystem factors unrelated to water quality. At higher loading rates, they found eelgrass coverage decreased markedly, with essentially no eelgrass presence at loading levels beyond $100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$.

¹⁶ Holmer et al. (2009) demonstrated that a benthic cover of certain species of the macroalga *Caulerpa* will cause high sediment sulphate reduction rates, to the detriment of the Mediterranean seagrass *Posidonia oceanica*.

¹⁷ Data provided in Tomasko et al. (2005) can be used to calculate a peak nitrogen loading rate in Tampa and Sarasota Bays (Florida) of roughly 70 to 80 $\text{kg N ha}^{-1} \text{ yr}^{-1}$. When loading rates were approximately halved in the 1980s, there was a resurgence in seagrass coverage in the bays.

V) Low Oxygen Levels

A reduction in dissolved oxygen concentration in the water column can come about from eutrophication (due to a greater biomass of respiring organisms in the water), poor flushing or mixing of a water mass, elevated water temperature, high concentrations of dissolved salts in the water, the addition of organic material or other 'oxygen demanding' chemicals from a point or non-point source, and other factors.

Eelgrass rhizomes can frequently be found growing in sediment with low oxygen concentrations. The plants accomplish this by supplying oxygen to the rhizomes via a well developed system of air spaces (lacunae) connecting leaves to plant tissues below the sediment surface. The lacunal system is more developed in plants growing in more anaerobic sediments (Penhale and Wetzel 1983).

Although seeds of eelgrass are capable of germinating under anoxic conditions (Churchill 1992), the seedlings will have unusual morphology. Holmer and Bondgaard (2001) used a three week laboratory experiment to demonstrate that photosynthetic and growth rates of *Z. marina* is inhibited under low oxygen conditions in the water column ($<63 \mu\text{M}$). Both photosynthesis and growth stopped if anoxic conditions were combined with high sulphide concentrations in the water (100 – 1000 μM). Holmer and Bondgaard (2001) provide enough information to allow an estimate of HADD thresholds for disruption, harmful alteration and destruction (Table 3).

The meristematic region of eelgrass leaves will quickly become anoxic if the water column is anoxic. This may be a key factor in seagrass die-off under low oxygen conditions (Greve et al. 2003).

Pulido and Borum (2010) performed laboratory experiments on the responses of *Zostera marina* to short term anoxia. Eelgrass ramets (terminal leaf bundles with rhizomes and roots) were submerged in anoxic seawater for variable periods of time (0.5 to 48 h) at three temperatures (20, 25 and 30 °C) in darkness. At 20 °C, negative effects of anoxia occurred after 12 (photosynthesis) and 24 hours (leaf growth). Shoot mortality occurred after 24 hours. The negative effects were much stronger at higher temperatures, with negative effects on photosynthesis, growth and survival after just a couple of hours of exposure to anoxia at 30 °C (Table 3).

A four day long bout of aquaculture related bottom water anoxia in a lagoon in south France caused the complete disappearance of local *Zostera marina* meadows (Plus et al. 2003). Recovery was relatively rapid (9 months) due to a replete seed bank and high seedling survival rate. As recovery was attained in this instance, we used these results to estimate a disruption threshold (Table 3).

Flow Regime

Species in the genus *Zostera* tend to grow best in low current regimes, although they can occur also on soft bottoms that are scoured to some extent by currents. Even non-scouring current regimes may have a negative effect on plant growth. Increasing current velocity from 5 to c.a. 12.5 cm s^{-1} led to a linear reduction in shoot number in *Z. noltii* from over 3500 shoots to less than 2500 shoots m^{-2} , along with reductions in leaf length (Schanz and Asmus 2003).

The 46 day mesocosm study of de los Santos et al. (2010) was already mentioned in the "turbidity" section above. They found that *Zostera noltii* shoots grown at saturating light intensity

had significantly reduced survival when grown under a current velocity of 10 or 35 cm s⁻¹ versus 1.0 cm s⁻¹ (Table 4)¹⁸.

Increasing current speed from 2 to 35-40 cm s⁻¹ increased leaf production in *Z. marina* (Fonseca and Kenworthy 1987), and it appears that eelgrass needs about ≥ 16 cm s⁻¹ of current for optimal conditions for photosynthesis (Koch 2001). See Table 4. Minimal current regimes may improve porewater geochemistry for seagrass growth (Koch 1999), or enhance nutrient uptake (Thomas and Cornelisen 2003; Morris et al. 2008).

Eelgrass is sensitive to wave action in shallow waters (van Katwijk and Hermus 2000; Koch 2001; van Katwijk and Wijgangers 2004); Krause-Jensen et al. (2003) provided data which indicate that the upper limit of eelgrass on shore may be determined by wave exposure, with stronger exposure limiting the beds to deeper waters. Shallow beds exposed to wave action will exhibit variable shape and position over time (Frederiksen et al. 2004b).

Eelgrass beds tend to have a lower proportion of seedlings as average current speeds increase. Current mediated movement of sediment may cause distinct ridges to form at the outer (current side) edges of the bed while wave scoured depression (i.e. blowouts) may occur inside the bed and migrate through it over time, producing a bed which may exhibit more vertical relief than the surrounding substrate. Under high energy, erosional conditions eelgrass beds can take on a 'leopard skin' or even donut or U shape depending upon the size and frequency of blowouts.

At near maximal current conditions for eelgrass, the beds will often turn into small, raised elliptical patches formed parallel to the current. The maximum current velocity regime for *Z. marina* is between 120 to 180 cm s⁻¹, although currents as low as ≤ 50 cm s⁻¹ may have negative effects (Fonseca et al. 1983; Fonseca and Kenworthy 1987; Koch 2001). See Table 4.

An abrupt transition point appears to exist for *Z. marina* at that current speed leading to 50% plant cover, ~ 25 cm s⁻¹. Above that current speed, eelgrass is unlikely to occur as contiguous beds (Fonseca and Bell 1998). See Table 4.

Physical Removal

Physical removal is a slightly different stressor from those discussed above, since removal itself is 'destruction' under the HADD terminology. Therefore, physical removals are evaluated here as a discussion of recovery rates and eelgrass bed integrity.

Seagrasses respond differently to different levels of physical removal. If the plants and rhizomes are disturbed by some physical activity but the bulk of the biomass is not removed, the plants can survive and recover quite well. This appears to be true for both *Zostera noltii* in Europe and *Z. marina* in North America (Boese 2002; Alexandre et al. 2005). Therefore, our discussion here focuses on complete physical removal of biomass.

Oyster aquaculture in the Pacific Northwest can occur on eelgrass beds. The oysters are sometimes harvested by dredging, which physically impacts the eelgrass beds. Tallis et al. (2009) monitored these effects and found up to a 56% reduction in eelgrass shoot density after such dredging operations. The beds recovered in approximately one year at one of the experimental sites, but another site still showed reduced density even four years later. The reasons for the difference in recovery rates between these sites were unknown (Table 5).

¹⁸ Using similar current regimes in the laboratory, Peralta et al. (2006) demonstrated that *Zostera noltii* responds to higher currents by becoming more robust and improving its anchoring system (roots and rhizomes).

Neckles et al. (2005) demonstrated severe impacts to *Z. marina* beds from commercial dredging for blue mussels (*Mytilus edulis*). Dredging impacts included removal of above and below ground eelgrass biomass. Eelgrass shoot density, shoot height and total biomass of disturbed sites were as low as <1% that of the reference sites. The impacts persisted up to 7 years after dredging. Neckles et al. (2005) projected that it would take approximately 10 yr for recovery to occur in areas of intense dragging (which were quite common). Recovery under conditions less conducive to eelgrass growth could require 20 yr or longer, constituting destruction for our purposes (Table 5).

Boese et al. (2009) removed *Z. marina* shoots in 4 m² experimental plots in lower intertidal perennial beds and higher intertidal patches. Even with the addition of seeds, recovery in the bare patches occurred exclusively due to rhizome growth from adjacent perennial eelgrass. It took two years for the bare patches to completely grow in at the lower intertidal site, and almost 34 months (the extent of the experimental observations) at the higher intertidal site (a sub-optimal location for eelgrass). These long recovery times constitute a harmful alteration for the purposes of HADD determinations (Table 5)¹⁹.

In Nova Scotia, eelgrass can be frozen to the underside of ice which ultimately breaks up into large pieces and floats away. In an experiment to mimic this ice scouring and rafting, Schneider and Mann (1991) created 1.2 X 0.4m bare patches in an eelgrass bed in spring. The size of the patches was chosen to match typical ice scour effects in the bed. Four months later, the biomass was still significantly lower in the cleared patches than in the surrounding eelgrass bed. The cleared patches had not completely regenerated 14 months later. Recovery of the experimental patches was entirely based upon regrowth from the edges, no seedlings were observed. Since the cleared patches did not regenerate within one year, this result would represent a harmful alteration (Table 5)²⁰.

The ice effect has caused an annual form of eelgrass to develop in Nova Scotia in shallow water areas subject to ice scour (<25cm depth at low tide). These annual plants do not survive the winter, do not develop much below sediment biomass, have high reproductive effort and overwinter as seeds (Robertson and Mann 1984).

Plus et al. (2003) observed the destruction of an eelgrass bed due to bottom water anoxia. Once the anoxic conditions had disappeared, the bed recovered within nine months due to a good seed bank in the sediment and high seedling survival²¹. In this instance, the damage could be considered a 'disruption' using HADD criteria (Table 5).

Note the predominant pattern we have described here - if eelgrass is physically removed but a good seed bank exists and good seedling survival is attained after the removal event, eelgrass beds may recover within a year. Under such conditions, the removal could be considered a 'disruption' under HADD. If, on the other hand the seed bank is low, recovery could take more than a year and the HADD would be due to a 'harmful alteration' - the bed would only recover through relatively slow growth of rhizomes through the sediment to fill the empty area²².

¹⁹ Di Carlo and Kenworthy (2008) record recovery times of only about 10% per year for bare patches in *Thalassia* meadows. The more opportunistic tropical seagrasses, *Syringodium* and *Halodule*, could recover in less than a year. Recovery was based on both seedlings and vegetative growth. Martin et al. (2008) estimate that propeller scars in *Halodule* beds could recover in less than three years.

²⁰ Badalamenti et al. (2006) describe long term harm to *Posidonia* from the construction of a pipeline trench.

²¹ Similar observations were made by Greve et al. (2005) where eelgrass dieback from anoxia led to recovery driven mainly by a large seed bank and seedlings.

²² In Newfoundland, experimental removal of eelgrass created 450 m² bare patches that took 3 to 7 years to recover based upon rhizome regrowth (Warren et al. 2010).

Vandermeulen (personal observation) has seen the intertidal annual (seed bank) form of *Zostera marina* as described by Robertson and Mann (1984), and the more 'vegetative growth' type of meadow expansion in subtidal eelgrass beds²³. As ice scour is quite common in Atlantic Canada, we may safely make the assumption that our intertidal beds of eelgrass may often be annual and subtidal beds perennial. If so, it may be prudent to take this into account when allowing project proponents to physically remove eelgrass, as removal in subtidal beds may lead to a harmful alteration.

Summary

Several aspects of stressors were considered to be important, including intensity, duration, area scale and frequency. These aspects were chosen to match the model used by managers when applying the HADD provisions of the Fisheries Act. Unfortunately, we found the majority of research studies are not designed to experimentally test for any of these particular aspects other than 'intensity' in a field situation on eelgrass. The columns for the other aspects could rarely be checked as 'yes' in any of our five tables.

The literature is full of studies on seagrasses that experimentally test for 'intensity' via altering and controlling for such factors as light intensity, nutrient loading rates, flow rates, and depth of burial. However, very few studies would also test and control for time based removal of excess sediment after burial (i.e. the duration aspect), or focus on alterations in current over some portion of an eelgrass bed (area scale), or pulsing excess nutrients over an eelgrass bed for specific times over a one year period (frequency). The existing seagrass research on impacts is not well matched with the requirements of managers determining or implementing HADD based decisions.

We had initially planned to focus on literature that measured eelgrass responses in terms of the habitat value of affected meadows. This desire to express values is why our five tables each have a column for the 'meadow level' responses of patchiness, shoot density, and area covered. We were somewhat successful with this approach, as many field based studies did measure shoot density. However, the responses of degree of patchiness and area covered were not measured frequently enough to generalize the studies.

Even with the shortcomings in the literature on aspects of a stressor and our focus on meadow responses, we were able to take each of our five tables and extract 'a best guess' of HADD thresholds²⁴. We suggest that these best guesses can form the basis of determining HADD thresholds, or at the very least a starting point for habitat managers (see summary in Table 6). Monitoring responses of eelgrass to each of the stressors can be tracked on a project by project basis to refine these suggested thresholds at various scales and geographic levels.

Sedimentation

The sedimentation thresholds cover burial and erosion of eelgrass beds, sedimentation, the presence of silt on leaves, and rhizome exposure. The secondary effects of sedimentation include water column turbidity and loss of light.

The suggested HADD thresholds on sedimentation in Table 6 are based upon data from *Zostera marina*, *Z. noltii* and *Z. capensis*. Only the first species occurs in Canada. The last two

²³ Boese et al. (2005) also report an annual form of *Zostera marina* in the higher intertidal of an estuary in Oregon, with perennial forms progressively dominating as one moves down to the lower intertidal.

²⁴ Recall that 'disruption' means the meadow can recover all of its structure and integrity within one year, while 'harmful alteration' refers to incomplete recovery taking more than a year.

species are temperate and generally smaller than the first and may be more sensitive to sedimentation than *Z. marina*. However, *Zostera* in general is very sensitive to sedimentation and it is best to prevent sediment deposition to protect the health of eelgrass beds at most spatial and temporal scales.

When considering HADD thresholds for sedimentation (or any other stressor for that matter) bear in mind the results of Sabol et al. (2005) whom found natural year-to-year variations in eelgrass cover in their particular bays obscured the meadow scale effects of sedimentation driven by dredging.

Turbidity

The suggested turbidity HADD thresholds in Table 6 include measures of Total Suspended Solids, percent of surface light, light attenuation coefficient ($K_d \text{ m}^{-1}$), moles of photons (quanta) $\text{m}^{-2} \text{ d}^{-1}$, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, and days of darkness (D) followed by days of light (L). Most of these measures of the turbidity stressor are problematic because they only indirectly gauge the true impact upon the seagrass meadow (i.e. light loss), which stems from leaf based loss of photosynthetic output.

For example, let's examine the values for 'percent of surface light' in Table 6. The measure refers to the proportion of light reaching the blades of the eelgrass compared to the light available at the surface of the water measured as Photosynthetic Photon Flux Density, Photosynthetically Available Radiation, or Irradiance. The values provided in Table 6 are a rough guide prepared by examining the values in Table 2.

The percent of surface light values in Table 6 are imprecise intentionally because the thresholds they represent can be confounded by the height of the eelgrass blades (the tips of tall blades receive light that the bases of the same blades may not 'see'), translocation of photosynthetic materials from shallow blade clusters to deeper ones by rhizomes (a light 'subsidy') and general photo-acclimation by eelgrass in chronically low light regimes (Lee et al. 2007). In other words, there is a disconnect between the percent of surface light values and the physiological responses of the seagrass from leaf to meadow scales.

This same disconnect exists for all of our turbidity measures except for "days of darkness" versus "days of light". The effect of darkness on photosynthesis is absolute, and therefore a clean measure of turbidity effects.

Once the photosynthetic rate drops due to turbidity, the stress upon the eelgrass bed may be compounded by its inability to provide enough oxygen via the lacunal system to continue to reoxidize sulphides in pore water, leading to pore water anoxia and excess sulphides. The deterioration in pore water quality at the plant's rhizomes and roots could lead to a cumulative negative feedback effect on eelgrass growth and survival (Holmer and Laursen 2002; Olivé et al. 2009). So, when considering the impacts of turbidity, some measure of pore water quality should be made as well.

The manager determining HADD stress effects on eelgrass from turbidity must also consider the indirect effect of epiphytes on the blades. Some measure of epiphyte cover must be made, either to provide a further estimate of light lost due to their presence on the blades (Hauxwell et al. 2001; Drake et al. 2003), or to model their influence on growth (Kemp et al. 2004).

Nutrients

The examination of nutrients as a stressor on eelgrass is even more problematic than turbidity effects. Adding nutrients to an eelgrass meadow leads to a host of secondary effects, all of which incrementally impact the meadows in different ways – including the generation of turbidity via phytoplankton blooms! The HADD threshold estimates provided in Table 6 must be carefully applied on a case by case basis, tracking all possible direct and indirect effects.

For direct effects, we focused upon nitrate and ammonium toxicity (Table 3 summarized in Table 6). Both water column and pore water values are provided in Table 6. Pore water values are more likely linked to direct toxicity than water column values, as the latter for any nutrient can be linked to a broader collection of secondary (i.e. non-toxic) effects like benthic macrophyte growth or increased epiphyte load.

There are a couple of factors which may alter the direct toxic effects of nitrate or ammonium on eelgrass. If the plants are nutritionally replete prior to exposure, the toxic effect may be greatly reduced (Brun et al. 2008). Meadow scale factors such as shoot density may also buffer any toxic effects (van der Heide et al. 2008).

The indirect effect of increased turbidity due to phytoplankton blooms from eutrophication has been mentioned above, this also holds for increased epiphyte load from eutrophication²⁵. Both of these eutrophication effects can be buffered by the presence of benthic and planktonic herbivores.

There are numerous instances of eelgrass beds in Atlantic Canada where moderate eutrophication effects are held in check by snails grazing epiphytes off of leaves (Vandermeulen, personal observation). It is often possible to see different locations in the same bay where epiphyte loads are high (snails rare) or epiphyte cover is very light (high snail density). Ultimately, if nutrient loading rates are locally high (e.g. fish packing plant outfall) benthic algae predominate, smothering out the eelgrass (see discussion below).

Another indirect effect of eutrophication is alteration of sediment geochemistry (e.g. elevated hydrogen sulphide). HADD thresholds for hydrogen sulphide in pore water are provided in Table 6. The range of values for 'disruption' is very wide, in part because short term acute effects on photosynthesis may be less sensitive than longer term growth effects due to hydrogen sulphide toxicity. Background water column oxygen status may also buffer the effects of pore water hydrogen sulphide toxicity (Pedersen et al. 2004).

The formation of benthic algal mats due to eutrophication also indirectly affects eelgrass growth and survival. The published literature on algal mats is quite consistent, and the values provided in Table 6 may be more helpful than other measures of nutrient stress. As for phytoplankton and epiphytes, the presence of herbivores can buffer benthic algal mat growth. Dense algal mats (filamentous algae) may have more harmful effects than loose algal mats (foliose forms). Algal mats stress eelgrass via shading, reducing oxygen levels, scouring the bottom and altering geochemistry.

Calculating nutrient loading rates for estuaries with eelgrass can be relatively straight forward and therefore appear tempting for habitat managers. However, loading rates are a surrogate measure of stress on eelgrass often many steps removed from the originating factors which ultimately impact eelgrass meadows in a particular location. We observed in the published

²⁵ Epiphytes stress eelgrass by shading it, as well as by interfering with nutrient and carbon uptake.

literature that there was a large variation in the loading rates associated with impacts on eelgrass beds. Therefore, the loading rate values (kg N ha^{-1} of estuary surface area yr^{-1}) provided in Table 6 should generally be used only as a rule of thumb to screen particular estuaries for further study.

Eutrophication is also often associated with reduced water column or pore water oxygen levels. The stress of low oxygen levels on eelgrass can be modulated by temperature, hydrogen sulphide concentrations and the partitioning of oxygen concentrations in the water column versus pore water. For simplicity, the threshold values provided in Table 6 are based upon hours of anoxia exposure at 20°C (Pulido and Borum 2010).

Flow Regime

Eelgrass (*Z. marina*) appears to require a minimal amount of current to survive, and will erode out completely under very energetic flow regimes. Between these two extremes, flow regime acts mainly to sculpt eelgrass meadow shape rather than stress the plants. The sculpting effect does increase patchiness and reduce the area covered by a meadow however, so this can be considered a "disruption" (Table 6). *Zostera noltii* has lower current tolerances than *Z. marina*.

Physical Removal

It was not possible to suggest HADD thresholds for the stress of physical removal. The effects span the full range of HADD criteria; from disruption through harmful alteration to destruction – all depending upon recovery rates. Recovery did not seem to be linked to the scale of the removal; entire meadows could re-grow quickly while small cleared patches may not.

Recovery rates seem to be driven by seed versus vegetative growth:

1. Fast recovery (i.e. less than a year, months)
 - a. large seed bank in sediment,
 - b. good seedling germination,
 - c. good seedling growth and survival
2. Slow recovery (i.e. years)
 - a. bare area fills in mainly via vegetative growth from adjacent rhizomes

In Atlantic Canada, recovery from seed banks appears to be quite important in certain intertidal environments where the annual form of eelgrass predominates (Robertson and Mann 1984). The same may be true for some intertidal sites on the Pacific coast (Boese et al. 2005). Subtidal eelgrass beds in Canada are more likely dominated by vegetative (rhizome-based) perennial growth. Recovery from physical removal will differ between the two types of beds as well as other unique location characteristics.

REFERENCES

- Abe, M., Hashimoto, N., Kurashima, A., and Maegawa, M. 2003. Estimation of light requirement for the growth of *Zostera marina* in central Japan. *Fisheries Science* 69: 890-895.
- Abe, M., Yokota, K., Kurashima, A., and Maegawa, M. 2010. Estimation of light requirement for growth of *Zostera japonica* cultured seedlings based on photosynthetic properties. *Fisheries Science* 76: 235-242.
- Alexandre, A., Santos, R., and Serrão, E. 2005. Effects of clam harvesting on sexual reproduction of the seagrass *Zostera noltii*. *Marine Ecology Progress Series* 298: 115-122.
- Apostolaki, E.T., Marbà, N., Holmer, M., and Karakassis, I. 2009. Fish farming enhances biomass and nutrient loss in *Posidonia oceanica* (L.) Delile. *Estuarine, Coastal and Shelf Science* 81: 390-400.
- Badalamenti, F., Di Carlo, G., D'Anna, G., Gristina, M., and Toccaceli, M. 2006. Effects of dredging activities on population dynamics of *Posidonia oceanica* (L.) Delile in the Mediterranean Sea: The case study of Capo Feto (SW Sicily, Italy). *Hydrobiologia* 555: 253-261.
- Biber, P.D., Kenworthy, W.J., and Paerl, H.W. 2009. Experimental analysis of the response and recovery of *Zostera marina* (L.) and *Halodule wrightii* (Ascher.) to repeated light-limitation stress. *Journal of Experimental Marine Biology and Ecology* 369: 110-117.
- Boese, B.L. 2002. Effects of recreational clam harvesting on eelgrass (*Zostera marina*) and associated infaunal invertebrates: In situ manipulative experiments. *Aquatic Botany* 73: 63-74.
- Boese, B.L., and Robbins, B.D. 2008. Effects of erosion and macroalgae on intertidal eelgrass (*Zostera marina*) in a northeastern Pacific estuary (USA). *Botanica Marina* 51: 247-257.
- Boese, B.L., Robbins, B.D., and Thursby, G. 2005. Desiccation is a limiting factor for eelgrass (*Zostera marina* L.) distribution in the intertidal zone of a northeastern Pacific (USA) estuary. *Botanica Marina* 48: 274-283.
- Boese, B.L., Kaldy, J.E., Clinton, P.J., Eldridge, P.M., and Folger, C.L. 2009. Recolonization of intertidal *Zostera marina* L. (eelgrass) following experimental shoot removal. *Journal of Experimental Marine Biology and Ecology* 374: 69-77.
- Boström, C., Roos, C., and Ronnberg, O. 2004. Shoot morphometry and production dynamics of eelgrass in the northern Baltic Sea. *Aquatic Botany* 79: 145-161.
- Boström, C., Bonsdorff, E., Kangas, P., and Norkko, A. 2002. Long-term changes of a brackish-water eelgrass (*Zostera marina* L.) community indicate effects of coastal eutrophication. *Estuarine, Coastal and Shelf Science* 55: 795-804.
- Bricelj, V.M., and Lonsdale, D.J. 1997. *Aureococcus anophagefferens*: Causes and ecological consequences of brown tides in U.S. mid-Atlantic coastal waters. *Limnology and Oceanography* 42: 1023-1038.

- Brun, F.G., Olivé, I., Malta, E.-j., Vergara, J.J., Hernández, I., and Pérez-Lloréns, J.L. 2008. Increased vulnerability of *Zostera noltii* to stress caused by low light and elevated ammonium levels under phosphate deficiency. *Marine Ecology Progress Series* 365: 67-75.
- Brush, M.J., and Nixon, S.W. 2002. Direct measurements of light attenuation by epiphytes on eelgrass *Zostera marina*. *Marine Ecology Progress Series* 238: 73-79.
- Burkholder, J.M., Glasgow, H.B. Jr., and Cooke, J.E. 1994. Comparative effects of water-column nitrate enrichment on eelgrass *Zostera marina*, shoalgrass *Halodule wrightii*, and widgeongrass *Ruppia maritima*. *Marine Ecology Progress Series* 105: 121-138.
- Burkholder, J.M., Mason, K.M., and Glasgow, H.B. Jr. 1992. Water-column nitrate enrichment promotes decline of eelgrass *Zostera marina*: evidence from seasonal mesocosm experiments. *Marine Ecology Progress Series* 81: 163-178.
- Cabaço, S., Machás, R., Vieira, V., and Santos, R. 2008. Impacts of urban wastewater discharge on seagrass meadows (*Zostera noltii*). *Estuarine, Coastal and Shelf Science* 78: 1-13.
- Cabello-Pasini, A., Lara-Turrent, C., and Zimmerman, R.C. 2002. Effect of storms on photosynthesis, carbohydrate content and survival of eelgrass populations from a coastal lagoon and the adjacent open ocean. *Aquatic Botany* 74: 149-164.
- Cabello-Pasini, A., Muñiz-Salazar, R., and Ward, D.H. 2003. Annual variations of biomass and photosynthesis in *Zostera marina* at its southern end of distribution in the North Pacific. *Aquatic Botany* 76: 31-47.
- Cancemi, G., DeFalco, G., and Pergent, G. 2003. Effects of organic matter input from a fish farming facility on a *Posidonia oceanica* meadow. *Estuarine, Coastal and Shelf Science* 56: 961-968.
- Cardoso, P.G., Leston, S., Grilo, T.F., Bordalo, M.D., Crespo, D., Raffaelli, D., and Pardal, M.A. 2010. Implications of nutrient decline in the seagrass ecosystem success. *Marine Pollution Bulletin* 60: 601-608.
- Carroll, J., Gobler, C.J., and Peterson, B.J. 2008. Resource-restricted growth of eelgrass in New York estuaries: Light limitation, and alleviation of nutrient stress by hard clams. *Marine Ecology Progress Series* 369: 51-62.
- Chambers, P.A., DeWreede, R.E., Irlandi, E.A., and Vandermeulen, H. 1999. Management issues in aquatic macrophyte ecology: A Canadian perspective. *Canadian Journal of Botany* 77: 471-487.
- Churchill, A.C. 1992. Growth characteristics of *Zostera marina* seedlings under anaerobic conditions. *Aquatic Botany* 43: 379-392.
- Collier, C.J., Lavery, P.S., Ralph, P.J., and Masini, R.J. 2009. Shade-induced response and recovery of the seagrass *Posidonia sinuosa*. *Journal of Experimental Marine Biology and Ecology* 370: 89-103.

- Cooper, S.R., and Brush, G.S. 1993. A 2,500 - year history of anoxia and eutrophication in Chesapeake Bay. *Estuaries* 16: 617-626.
- Cooper, S.R., McGlothlin, S.K., Madritch, M., and Jones, D.L. 2004. Paleoecological evidence of human impacts on the Neuse and Pamlico estuaries of North Carolina, USA. *Estuaries* 27: 617-633.
- Cummins, S.P., Roberts, D.E., and Zimmerman, K.D. 2004. Effects of the green macroalga *Enteromorpha intestinalis* on macrobenthic and seagrass assemblages in a shallow coastal estuary. *Marine Ecology Progress Series* 266: 77-87.
- Cyrus, D.P., MacKay, C.F., and Weerts, S.P. 2008. Intrusion of beach-disposed dredger spoil into the Mhlathuze Estuary, South Africa, and its impact on *Zostera capensis*. *African Journal of Aquatic Science* 33: 223-231.
- Daniell, J.J., Harris, P.T., Hughes, M.G., Hemer, M., and Heap, A. 2008. The potential impact of bedform migration on seagrass communities in Torres Strait, northern Australia. *Continental Shelf Research* 28: 2188-2202.
- De Falco, G., Baroli, M., Murru, E., Piergallini, G., and Cancemi, G. 2006. Sediment analysis evidences two different depositional phenomena influencing seagrass distribution in the Gulf of Oristano (Sardinia, Western Mediterranean). *Journal of Coastal Research* 22: 1043-1050.
- de los Santos, C.B., Brun, F.G., Bouma, T.J., Vergara, J.J., and Pérez-Lloréns, J.L. 2010. Acclimation of seagrass *Zostera noltii* to co-occurring hydrodynamic and light stresses. *Marine Ecology Progress Series* 398: 127-135.
- de Wit, R., Stal, L.J., Lomstein, B.A., Herbert, R.A., van Gemerden, H., Viaroli, P., Cecherelli, V.U., Rodriguez-Valera, F., Bartoli, M., Giordani, G., Azzoni, R., Schaub, B., Welsh, D.T., Donnelly, A., Cifuentes, A., Anton, J., Finster, K., Nielsen, L.B., Pedersen, A.G.U., Neubauer, A.T., Colangelo, M.A., and Heijs, S.K. 2001. ROBUST: The ROle of BUffering capacities in STabilising coastal lagoon ecosystems. *Continental Shelf Research* 21: 2021-2041.
- Deegan, L.A., Wright, A., Ayzasian, S.G., Finn, J.T., Golden, H., Merson, R.R., and Harrison, J. 2002. Nitrogen loading alters seagrass ecosystem structure and support of higher trophic levels. *Aquatic Conservation: Marine and Freshwater Ecosystems* 12: 193-212.
- den Hartog, C. 1970. Sea-grasses of the world. North-Holland Publishing Company, Amsterdam, The Netherlands.
- Di Carlo, G., and Kenworthy, W.J. 2008. Evaluation of aboveground and belowground biomass recovery in physically disturbed seagrass beds. *Oecologia* 158: 285-298.
- Dolbeth, M., Pardal, M.A., Lillebo, A.I., Azeiteiro, U., and Marques, J.C. 2003. Short- and long-term effects of eutrophication on the secondary production of an intertidal macrobenthic community. *Marine Biology* 143: 1229-1238.
- Drake, L.A., Dobbs, F.C., and Zimmerman, R.C. 2003. Effects of epiphyte load on optical properties and photosynthetic potential of the seagrasses *Thalassia testudinum* Banks ex König and *Zostera marina* L. *Limnology and Oceanography* 48: 456-463.

- Duarte, C.M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41: 87-112.
- Duarte, C.M. 2002. The future of seagrass meadows. *Environmental Conservation* 29: 192-206.
- Duffy, J.E., and Harvilicz, A.M. 2001. Species-specific impacts of grazing amphipods in an eelgrass-bed community. *Marine Ecology Progress Series* 223: 201-211.
- Erftemeijer, P.L.A., and Lewis, R.R.R. III. 2006. Environmental impacts of dredging on seagrasses: A review. *Marine Pollution Bulletin* 52: 1553-1572.
- Everett, R.A., Ruiz, G.M., and Carlton, J.T. 1995. Effect of oyster mariculture on submerged aquatic vegetation: An experimental test in a Pacific Northwest estuary. *Marine Ecology Progress Series* 125: 205-217.
- Fonseca, M.S., and Bell, S.S. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Marine Ecology Progress Series* 171: 109-121.
- Fonseca, M.S., and Kenworthy, W.J. 1987. Effects of current on photosynthesis and distribution of seagrasses. *Aquatic Botany* 27: 59-78.
- Fonseca, M.S., Zieman, J.C., Thayer, G.W., and Fisher, J.S. 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. *Estuarine, Coastal and Shelf Science* 17: 367-380.
- Fox, S.E., Stieve, E., Valiela, I., Hauxwell, J., and McClelland, J. 2008. Macrophyte abundance in Waquoit Bay: Effects of land-derived nitrogen loads on seasonal and multi-year biomass patterns. *Estuaries and Coasts* 31: 532-541.
- Frederiksen, M., Krause-Jensen, D., Holmer, M., and Laursen, J.S. 2004. Long-term changes in area distribution of eelgrass (*Zostera marina*) in Danish coastal waters. *Aquatic Botany* 78: 167-181.
- Frederiksen, M., Krause-Jensen, D., Holmer, M., and Laursen, J.S. 2004b. Spatial and temporal variation in eelgrass (*Zostera marina*) landscapes: Influence of physical setting. *Aquatic Botany* 78: 147-165.
- Goodman, J.L., Moore, K.A., and Dennison, W.C. 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. *Aquatic Botany* 50: 37-47.
- Greve, T.M., Borum, J., and Pedersen, O. 2003. Meristematic oxygen variability in eelgrass (*Zostera marina*). *Limnology and Oceanography* 48: 210-216.
- Greve, T.M., Krause-Jensen, D., Rasmussen, M.B., and Christensen, P.B. 2005. Means of rapid eelgrass (*Zostera marina* L.) recolonization in former dieback areas. *Aquatic Botany* 82: 143-156.
- Harlin, M.M., and Thorne-Miller, B. 1981. Nutrient enrichment of seagrass beds in a Rhode Island coastal lagoon. *Marine Biology* 65: 221-229.

- Hauxwell, J., Cebrian, J., and Valiela, I. 2003. Eelgrass *Zostera marina* loss in temperate estuaries: Relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series* 247: 59-73.
- Hauxwell, J., Cebrian, J., and Valiela, I. 2006. Light dependence of *Zostera marina* annual growth dynamics in estuaries subject to different degrees of eutrophication. *Aquatic Botany* 84: 17-25.
- Hauxwell, J., Cebrian, J., Furlong, C., and Valiela, I. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* 82: 1007-1022.
- Hebert, A.B., and Morse, J.W. 2003. Microscale effects of light on H₂S and Fe²⁺ in vegetated (*Zostera marina*) sediments. *Marine Chemistry* 81: 1-9.
- Hily, C., Connan, S., Raffin, C., and Wyllie-Echeverria, S. 2004. In vitro experimental assessment of the grazing pressure of two gastropods on *Zostera marina* L. ephyphitic algae. *Aquatic Botany* 78: 183-195.
- Holmer, M., and Bondgaard, E.J. 2001. Photosynthetic and growth response of eelgrass to low oxygen and high sulfide concentrations during hypoxic events. *Aquatic Botany* 70: 29-38.
- Holmer, M., and Laursen, L. 2002. Effect of shading of *Zostera marina* (eelgrass) on sulfur cycling in sediments with contrasting organic matter and sulfide pools. *Journal of Experimental Marine Biology and Ecology* 270: 25-37.
- Holmer, M., and Nielsen, R.M. 2007. Effects of filamentous algal mats on sulfide invasion in eelgrass (*Zostera marina*). *Journal of Experimental Marine Biology and Ecology* 353: 245-252.
- Holmer, M., Baden, S., Boström, C., and Moksnes, P-O. 2009b. Regional variation in eelgrass (*Zostera marina*) morphology, production and stable sulfur isotopic composition along the Baltic Sea and Skagerrak coasts. *Aquatic Botany* 91: 303-310.
- Holmer, M., Marbà, N., Lamote, M., and Duarte, C.M. 2009. Deterioration of sediment quality in seagrass meadows (*Posidonia oceanica*) invaded by macroalgae (*Caulerpa* sp.). *Estuaries and Coasts* 32: 456-466.
- Holmer, M., Pedersen, O., Krause-Jensen, D., Olesen, B., Petersen, M.H., Schopmeyer, S., Koch, M., Lomstein, B.A., and Jensen, H.S. 2009c. Sulfide intrusion in the tropical seagrasses *Thalassia testudinum* and *Syringodium filiforme*. *Estuarine, Coastal and Shelf Science* 85: 319-326.
- Houk, P., and Camacho, R. 2010. Dynamics of seagrass and macroalgal assemblages in Saipan Lagoon, Western Pacific Ocean: Disturbances, pollution, and seasonal cycles. *Botanica Marina* 53: 205-212.
- Kaldy, J.E., Dunton, K.H., Kowalski, J.L., and Lee, K-S. 2004. Factors controlling seagrass revegetation onto dredged material deposits: A case study in lower Laguna Madre, Texas. *Journal of Coastal Research* 20: 292-300.

- Karez, R., Engelbert, S., Kraufvelin, P., Pedersen, M.F., and Sommer, U. 2004. Biomass response and changes in composition of ephemeral macroalgal assemblages along an experimental gradient of nutrient enrichment. *Aquatic Botany* 78: 103-117.
- Kemp, W.M., Batiuk, R., Bartleson, R., Bergstrom, P., Carter, V., Gallegos, C.L., Huntley, W., Karrh, L., Koch, E.W., Landwehr, J.M., Moore, K.A., Murray, L., Naylor, M., Rybicki, N.B., Stevenson, J.C., and Wilcox, D.J. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water quality, light regime, and physical-chemical factors. *Estuaries* 27: 363-377.
- Koch, E.W. 1999. Preliminary evidence on the interdependent effect of currents and porewater geochemistry on *Thalassia testudinum* Banks ex König seedlings. *Aquatic Botany* 63: 95-102.
- Koch, E.W. 2001. Beyond light: Physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24: 1-17.
- Krause-Jensen, D., Pedersen, M.F., and Jensen, C. 2003. Regulation of eelgrass (*Zostera marina*) cover along depth gradients in Danish coastal waters. *Estuaries* 26: 866-877.
- Latimer, J.S., and Rego, S.A. 2010. Empirical relationship between eelgrass extent and predicted watershed-derived nitrogen loading for shallow New England estuaries. *Estuarine, Coastal and Shelf Science* 90: 231-240.
- Laurel, B.J., Gregory, R.S., and Brown, J.A. 2003. Predator distribution and habitat patch area determine predation rates on Age-0 juvenile cod *Gadus* spp. *Marine Ecology - Progress Series* 251:245-254.
- Lee, K-S., Park, S.R., and Kim, Y.K. 2007. Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: A review. *Journal of Experimental Marine Biology and Ecology* 350: 144-175.
- Lee, K-S., Short, F.T., and Burdick, D.M. 2004. Development of a nutrient pollution indicator using seagrass, *Zostera marina*, along nutrient gradients in three New England estuaries. *Aquatic Botany* 78: 197-216.
- Lee, S.Y. 1997. Annual cycle of biomass of a threatened population of the intertidal seagrass *Zostera japonica* in Hong Kong. *Marine Biology* 129: 183-193.
- Leoni, V., Vela, A., Pasqualini, V., Pergent-Martini, C., and Pergent, G. 2008. Effects of experimental reduction of light and nutrient enrichments (N and P) on seagrasses: A review. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18: 202-220.
- Leston, S., Lillebø, A.I., and Pardal, M.A. 2008. The response of primary producer assemblages to mitigation measures to reduce eutrophication in a temperate estuary. *Estuarine, Coastal and Shelf Science* 77: 688-696.
- Lillebø, A.I., Neto, J.M., Martins, I., Verdelhos, T., Leston, S., Cardoso, P.G., Ferreira, S.M., Marques, J.C., and Pardal, M.A. 2005. Management of a shallow temperate estuary to control eutrophication: The effect of hydrodynamics on the system's nutrient loading. *Estuarine, Coastal and Shelf Science* 65: 697-707.

- Lotze, H.K., Milewski, I., Worm, B., and Koller, Z. 2003. Nutrient pollution: a eutrophication survey of eelgrass beds in estuaries and coastal bays in northern and eastern New Brunswick. Conservation Council of New Brunswick, Fredericton. 60pp.
- Marsh, J.A. Jr., Dennison, W.C., and Alberte R.S. 1986. Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina* L.). Journal of Experimental Marine Biology and Ecology 101: 257-267.
- Martin, S.R., Onuf, C.P., and Dunton, K.H. 2008. Assessment of propeller and off-road vehicle scarring in seagrass beds and wind-tidal flats of the southwestern Gulf of Mexico. Botánica Marina 51: 79-91.
- Martínez-Lüscher, J., and Holmer, M. 2010. Potential effects of the invasive species *Gracilaria vermiculophylla* on *Zostera marina* metabolism and survival. Marine Environmental Research 69: 345-349.
- Mills, K.E., and Fonseca, M.S. 2003. Mortality and productivity of eelgrass *Zostera marina* under conditions of experimental burial with two sediment types. Marine Ecology Progress Series 255: 127-134.
- Moore, K.A., Neckles, H.A., and Orth, R.J. 1996. *Zostera marina* (eelgrass) growth and survival along a gradient of nutrients and turbidity in the lower Chesapeake Bay. Marine Ecology Progress Series 142: 247-259.
- Morris, E.P., Peralta, G., Brun, F.G., van Duren, L., Bouma, T.J., and Perez-Llorens, J.L. 2008. Interaction between hydrodynamics and seagrass canopy structure: Spatially explicit effects on ammonium uptake rates. Limnology and Oceanography 53: 1531-1539.
- Neckles, H.A., Short, F.T., Barker, S., and Kopp, B.S. 2005. Disturbance of eelgrass *Zostera marina* by commercial mussel *Mytilus edulis* harvesting in Maine: Dragging impacts and habitat recovery. Marine Ecology Progress Series 285: 57-73.
- Newell, R.I.E., and Koch, E.W. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. Estuaries 27: 793-806.
- Nixon, S.W. 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. Ophelia 41: 199-219.
- Ochieng, C.A., Short, F.T., and Walker, D.I. 2010. Photosynthetic and morphological responses of eelgrass (*Zostera marina* L.) to a gradient of light conditions. Journal of Experimental Marine Biology and Ecology 382: 117-124.
- Olivé, I., García-Sánchez, M.P., Brun, F.G., Vergara, J.J., and Pérez-Lloréns, J.L. 2009. Interactions of light and organic matter under contrasting resource simulated environments: the importance of clonal traits in the seagrass *Zostera noltii*. Hydrobiologia 629: 199-208.
- Patricio, J., Ulanowicz, R., Pardal, M.A., and Marques, J.C. 2004. Ascendancy as an ecological indicator: A case study of estuarine pulse eutrophication. Estuarine, Coastal and Shelf Science 60: 23-35.

- Pedersen, M.F. 1995. Nitrogen limitation of photosynthesis and growth: Comparison across aquatic plant communities in a Danish estuary (Roskilde Fjord). *Ophelia* 41: 261-272.
- Pedersen, M.F., and Borum, J. 1992. Nitrogen dynamics of eelgrass *Zostera marina* during a late summer period of high growth and low nutrient availability. *Marine Ecology Progress Series* 80: 65-73.
- Pedersen, O., Binzer, T., and Borum, J. 2004. Sulphide intrusion in eelgrass (*Zostera marina* L.). *Plant, Cell and Environment* 27: 595-602.
- Penhale, P.A., and Wetzel, R.G. 1983. Structural and functional adaptations of eelgrass (*Zostera marina* L.) to the anaerobic sediment environment. *Canadian Journal of Botany* 61: 1421-1428.
- Peralta, G., Brun, F.G., Pérez-Lloréns, J.L., and Bouma, T.J. 2006. Direct effects of current velocity on the growth, morphometry and architecture of seagrasses: A case study on *Zostera noltii*. *Marine Ecology Progress Series* 327: 135-142.
- Peralta, G., Bouma, T.J., van Soelen, J., Perez-Llorens, J.L., and Hernandez, I. 2003. On the use of sediment fertilization for seagrass restoration: A mesocosm study on *Zostera marina* L. *Aquatic Botany* 75: 95-110.
- Philippart, J.M. 1995. Effects of shading on growth, biomass and population maintenance of the intertidal seagrass *Zostera noltii* Hornem in the Dutch Wadden Sea. *Journal of Experimental Marine Biology and Ecology* 188: 199-213.
- Plus, M., Deslous-Paoli, J-M., and Degault, F. 2003. Seagrass (*Zostera marina* L.) bed recolonization after anoxia-induced full mortality. *Aquatic Botany* 77: 121-134.
- Pulido, C., and Borum, J. 2010. Eelgrass (*Zostera marina*) tolerance to anoxia. *Journal of Experimental Marine Biology and Ecology* 385: 8-13.
- Robertson, A.I., and Mann, K.H. 1984. Disturbance by ice and life-history adaptations of the seagrass *Zostera marina*. *Marine Biology* 80: 131-141.
- Rozan, T.F., Taillefert, M., Trouwborst, R.E., Glazer, B.T., Ma, S., Herszage, J., Valdes, L.M., Price, K.S., and Luther, G.W. III. 2002. Iron-sulfur-phosphorus cycling in the sediments of a shallow coastal bay: implications for sediment nutrient release and benthic macroalgal blooms. *Limnology and Oceanography* 47: 1346-1354.
- Sabol, B., Shafer, D., and Lord, E. 2005. Dredging effects on eelgrass (*Zostera marina*) distribution in a New England small boat harbor. US Army Corps of Engineers, Engineer Research and Development Center, Environmental Laboratory. Technical Report TR-05-8.
- Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquatic Botany* 3: 55-63.
- Schanz, A., and Asmus, H. 2003. Impact of hydrodynamics on development and morphology of intertidal seagrasses in the Wadden Sea. *Marine Ecology Progress Series* 261: 123-134.

- Schneider, F.I., and Mann, K.H. 1991. Rapid recovery of fauna following simulated ice rafting in a Nova Scotian seagrass bed. *Marine Ecology Progress Series* 78: 57-70.
- Sfriso, A., and Marcomini, A. 1999. Macrophyte production in a shallow coastal lagoon. Part II: Coupling with sediment, SPM and tissue carbon, nitrogen and phosphorus concentrations. *Marine Environmental Research* 47: 285-309.
- Short, F.T., and Burdick, D.M. 1996. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts. *Estuaries* 19: 730-739.
- Short, F.T., and Wyllie-Echeverria, S. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23: 17-27.
- Short, F.T., Burdick, D.M., and Kaldy, J.E. III. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. *Limnology and Oceanography* 40: 740-749.
- Short, F.T., Coles, R.G., and Short C.A. 2001. *Global seagrass research methods*. Elsevier Science. Amsterdam, The Netherlands.
- Sugimoto, K., Hiraoka, K., Ohta, S., Niimura, Y., Terawaki, T., and Okada, M. 2007. Effects of ulvoid (*Ulva* spp.) accumulation on the structure and function of eelgrass (*Zostera marina* L.) bed. *Marine Pollution Bulletin* 54: 1582-1585.
- Tallis, H.M., Ruesink, J.L., Dumbauld, B., Hacker, S., and Wisheart, L.M. 2009. Oysters and aquaculture practices affect eelgrass density and productivity in a Pacific Northwest estuary. *Journal of Shellfish Research* 28: 251-261.
- Tamaki, H., Tokuoka, M., Nishijima, W., Terawaki, T., and Okada, M. 2002. Deterioration of eelgrass, *Zostera marina* L., meadows by water pollution in Seto Inland Sea, Japan. *Marine Pollution Bulletin* 44: 1253-1258.
- Terrados, J., Duarte, C.M., Kamp-Nielsen, L., Agawin, N.S.R., Gacia, E., Lacap, D., Fortes, M.D., Borum, J., Lubanski, M., and Greve, T. 1999. Are seagrass growth and survival constrained by the reducing conditions of the sediment? *Aquatic Botany* 65: 175-197.
- Thom, R.M., and Southard, S.L. 2008. Light requirements for growth and survival of eelgrass (*Zostera marina* L.) in Pacific Northwest (USA) estuaries. *Estuaries and Coasts* 31: 969-980.
- Thomas, F.I.M., and Cornelisen, C.D. 2003. Ammonium uptake by seagrass communities: effects of oscillatory versus unidirectional flow. *Marine Ecology Progress Series* 247: 51-57.
- Tomasko, D.A., Corbett, C.A., Greening, H.S., and Raulerson, G.E. 2005. Spatial and temporal variation in seagrass coverage in Southwest Florida: Assessing the relative effects of anthropogenic nutrient load reductions and rainfall in four contiguous estuaries. *Marine Pollution Bulletin* 50: 797-805.

- Touchette, B.W., Burkholder, J.M., and Glasgow, H.B. Jr. 2003. Variations in eelgrass (*Zostera marina* L.) morphoogy and internal nutrient composition as influenced by increased temperature and water column nitrate. *Estuaries* 26: 142-155.
- Udy, J.W., and Dennison, W.C. 1997. Physiological responses of seagrasses used to identify anthropogenic nutrient inputs. *Marine and Freshwater Research* 48: 605-614.
- Valdemarsen, T., Canal-Vergés, P., Kristensen, E., Holmer, M., Kristiansen, M.D., and Flindt, M.R. 2010. Vulnerability of *Zostera marina* seedlings to physical stress. *Marine Ecology Progress Series* 418: 119-130.
- van der Heide, T., Peeters, E.T.H.M., Hermus, D.C.R., van Katwijk, M.M., Roelofs, J.G.M., and Smolders, A.J.P. 2009. Predicting habitat suitability in temperate seagrass ecosystems. *Limnology and Oceanography* 54: 2018-2024.
- van der Heide, T., Smolders, A.J.P., Rijkens, B.G.A., van Nes, E.H., van Katwijk, M.M., and Roelofs, J.G.M. 2008. Toxicity of reduced nitrogen in eelgrass (*Zostera marina*) is highly dependent on shoot density and pH. *Oecologia* 158: 411-419.
- van der Heide, T., Bouma, T.J., van Nes, E.H., van de Koppel, J., Scheffer, M., Roelofs, J.G.M., van Katwijk, M.M., and Smolders, A.J.P. 2010. Spatial self-organized patterning in seagrasses along a depth gradient of an intertidal ecosystem. *Ecology* 91: 362-369.
- van Katwijk, M.M., and Hermus, D.C.R. 2000. Effects of water dynamics on *Zostera marina*: Transplantation experiments in the intertidal Dutch Wadden Sea. *Marine Ecology Progress Series* 208: 107-118.
- van Katwijk, M.M., and Wijgergangs, L.J.M. 2004. Effects of locally varying exposure, sediment type and low-tide water cover on *Zostera marina* recruitment from seed. *Aquatic Botany* 80: 1-12.
- van Katwijk, M.M., Schmitz, G.H.W., Gasseling, A.P., and van Avesaath, P.H. 1999. Effects of salinity and nutrient load and their interaction on *Zostera marina*. *Marine Ecology Progress Series* 190: 155-165.
- Vandermeulen, H. 2005. Assessing marine habitat sensitivity: A case study with eelgrass (*Zostera marina* L.) and kelps (*Laminaria*, *Macrocystis*). DFO Can. Sci. Advis. Sec. Res. Doc. 2005/032, 57 pp.
- Vandermeulen, H. 2009. An introduction to eelgrass (*Zostera marina* L.): The persistent ecosystem engineer. Fisheries and Oceans, DFO Can. Sci. Advis. Sec. Res. Doc. 2009/085, 11pp.
- Vandermeulen, H., Jamieson, G., and Ouellette, M. 2006. Shellfish aquaculture and marine habitat sensitivity case studies. DFO Can. Sci. Advis. Sec. Res. Doc. 2006/036, 62 pp.
- Vaudrey, J.M.P., Kremer, J.N., Branco, B.F., and Short, F.T. 2010. Eelgrass recovery after nutrient enrichment reversal. *Aquatic Botany* 93: 237-243.
- Ward, D.H., Morton, A., Tibbitts, T.L., Douglas, D.C., and Carrera-González, E. 2003. Long-term change in eelgrass distribution at Bahía San Quintín, Baja California, Mexico, using satellite imagery. *Estuaries* 26: 1529-1539.

- Warren, M.A., Gregory, R.S., Laurel, B.J., and Snelgrove, P.V.R. 2010. Increasing density of juvenile Atlantic (*Gadus morhua*) and Greenland cod (*G. ogac*) in association with spatial expansion and recovery of eelgrass (*Zostera marina*) in a coastal nursery habitat. *Journal of Experimental Marine Biology and Ecology* 394: 154-160.
- Williams, S.L., and Ruckelshaus, M.H. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology* 74: 904-918.